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General Editors: G. R. DE BEER and MICHAEL ABERCROMBIE

PLANT ECOLOGY

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PLANT ECOLOGY

FOR THE STUDENT OF BRITISH VEGETATION

BY

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WITH SIX ILLUSTRATIONS

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PREFACE

THE aim of this book is to provide the student of British vegetation with a concise account of the aims and principles of Plant Ecology and to serve as a guide to the carrying out of field work in a scientific manner. Stress has been laid by the author only on those aspects of the subject, which in the light of modern tendencies appear to be definitely progressive. In this connexion it has been considered advisable to devote a comparatively large section of the book to the discussion of soil problems. In view of the great advances that have been made in the study of soil science in recent years, and because of the predominating influence of soil factors on most types of vegetation, this should be particularly welcome.

No attempt has been made to cater for any particular category of student. The object throughout the book has been to give a clear and easily understandable account of both theoretical and practical sides of plant ecology, with a view to meeting to some extent the needs of the school, the training college and the university alike. As, in a volume of the size of the present one, it would be obviously impossible to treat exhaustively even one aspect of the subject, the more advanced student will naturally find it necessary from time to time to supplement his reading on particular points by referring to other works. Only a very limited number of references has been given, but in those will be found bibliographies which should adequately meet most requirements.

I wish to express my indebtedness and thanks to Professor A. G. Tansley, for helpful criticism and valuable suggestions in relation to many of the points dealt with throughout this book. My thanks also are due to Mr. W. Morley Davies for reading through and criticizing the section on edaphic factors. I am also indebted to those writers on soil problems, whose works I have cited and made considerable use of as sources of information.

W. L.

BIRMINGHAM, *Jan., 1933*

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PLANT ECOLOGY

CHAPTER I

INTRODUCTORY

AIMS AND SCOPE OF PLANT ECOLOGY

AS the word implies, ecology is the study of home conditions and plant ecology is therefore that aspect of botanical science which concerns itself with the home lives, so to speak, of plants. It is consequently, for the greater part, an outdoor study and may in some measure be regarded as a modern development of what has long been known as field botany. In the old days the field botanist was almost entirely a systematist, and his activities were usually confined solely to the collecting, naming and recording of the localities of the plants he found growing during his rambles through the countryside. As will be seen later, the activities of the ecologist cover a much wider field. Although he must be to some extent a systematist, his chief problems are really problems of plant physiology, and allied sciences such as soil chemistry and soil physics may also frequently be involved. In spite of this, the study of plant ecology is often pursued as if it were a somewhat isolated and self-contained branch of botany, the ultimate aims of which are reached when the presence, and frequency of occurrence, of the various plant species growing on a vegetation-covered area are recorded, and a more or less approximately accurate estimate is made of the more obvious environmental conditions under which the plants are existing. This somewhat superficial conception of the subject, while excusable in the early days of plant ecology, is quite out of keeping with the modern progressive tendencies of biological science, but in spite of this it still persists in certain quarters, though happily in a diminishing degree.

When, however, we consider the scope of plant ecology from a scientific standpoint, we must inevitably arrive at the conclusion that, instead of being a minor branch of botanical science, it is actually one of its future main lines of advance. We want to know how and why plants grow as they do in the field, and we want to know how we can control their activities with certainty. These are the chief aims of the plant ecologist, they are also largely the aims of the plant physiologist. The physiologist uses experimental methods and carries out most of his work in the laboratory. Practically all the knowledge gained by the physiologist has direct bearing upon ecological problems, in fact, real advance in plant ecology largely depends upon advance in plant physiology. Ultimately, much experimental work in plant physiology will have to be carried out under natural conditions in the field, and when this comes about, plant ecology and plant physiology will be synonymous. Although it may be long before these two converging lines of investigation become completely united in this way, the fact remains that the ultimate aims of both are the same. They are both working towards a complete understanding of the vital activities of plants.

Until recently, ecologists have tended, for the greater part, to work purely on observational and descriptive lines. This has been largely due to two causes. In the first place a great deal of preliminary work, which may be termed morphological, on the external features and composition of vegetation has been necessary, and, in fact, there is still a certain amount of such work to be done. In the second place, although most workers fully realize the importance of obtaining accurate data concerning the environmental conditions under which plants grow in the field, and concerning the physiological relationships between the plants and these environmental conditions, or habitat factors as they are termed, the lack of suitable experimental methods for use in the field seriously hampers progress. We shall see in a later section of this book, that a certain amount of experimental work can be conveniently carried out in the field, but the fact remains that a satisfactory rate of progress in ecological work will not be realized until an improved and refined experimental technique, which is convenient for use in the field, has been evolved.

In regard to field methods, workers in agricultural research, whose problems are largely ecological, are in many ways far ahead of the pure ecologist, a fact which calls for a closer association between the two. Such a state of affairs in which the pure scientist is in the position of following the lead of the applied scientist is somewhat anomalous, and certainly suggests the need for greater exertion on the part of the ecologist.

From what has been said above, it will be readily understood that plant ecology if studied along progressive lines is pre-eminently of a practical nature. It is impossible to over-emphasize the necessity of intimate investigation into the nature and physiological effects of habitat factors. Descriptive work in which only the composition and distribution of various types of vegetation are dealt with cannot be regarded as more than preliminary in character. The real aim of the subject is thus eventually to explain fully why certain plants grow and are associated together in particular situations and why they do not grow in others. The problems involved include both the identification of the various operating habitat factors and an estimation of their intensities, and investigation of the ways in which these factors actually affect the plants physiologically. In such work it may be necessary to consider the vegetation type as a whole, or to deal with the different species individually. It should be needless to point out to the student the futility of merely making superficial examinations of various examples of a given type of vegetation as they occur at various places, in the hope that the reasons for the existence of such a type will eventually reveal themselves.

With regard to the actual carrying out of ecological work, one would point out that this need not be prevented by the fact that the student does not reside within easy reach of areas covered with more or less natural vegetation. It is true that such areas are pleasant to work in and undoubtedly have an attraction for most field workers, but if only agricultural land is available, or if the only near-by vegetation is that colonizing the pit mounds in a mining district, there are problems relating to the interactions between plants and their environment, the attempted solution of which will afford valuable and interesting fields for study.

CHAPTER II

THE PRINCIPLES OF PLANT ECOLOGY

PLANT COMMUNITIES

ONE of the most characteristic things about plants growing in the field under more or less natural conditions is the fact that they are always associated together in what we term plant communities. This was recognized long before ecology, or even botany, was thought of, as is obvious from the universal understanding of what is meant, for example, by such expressions as an oak wood, a pine wood, or a heather moor. These plant communities each have special features which differentiate them one from another. In an oak wood, for instance, in addition to the oak trees which give rise to the name, one expects to find, and does find, certain other characteristic plants, and in the same way one associates other plants besides heather with a heather moor. Even the most pronounced non-botanical person looks in an oak wood for bluebells and does not seek them on moorland. The various types of plant communities resemble or differ from each other in different ways and to different degrees. For example, we have various kinds of woodland such as oak wood, pine wood, ash wood, or beech wood. These all resemble each other in that in each the most characteristic species present are trees, but they differ from each other in that these characteristic species are oak, pine, ash, and beech respectively. These characteristic species are termed by ecologists the *dominant* species of the communities, but as other questions are involved in connexion with dominance we shall have occasion to speak of it again at greater length. Thus, two plant communities may differ from each other in respect of their dominant species, they may also resemble each other in that the dominant species in both cases may be trees, or shrubs or herbs, or in other words, are of the same life form. The life forms of the various plants which go to make up the community play an important part in determining its general structure. In a grassland community all the species present are herbs and are approximately equal in size, but on a stretch of moorland where the dominant species is the ling (*Calluna vulgaris*), which is a shrub, we often find small herbaceous plants growing in the shade of the *Calluna*. The foliage of the dominant *Calluna* and of the herbs beneath it form, as it were, two separate layers or strata. This stratification of vegetation in a community often becomes more complex if the dominant species are trees, and we may often find plants of various degrees of tallness associated together and forming three or four strata, one above another. This difference in life form possessed by different species is one of the factors which enables them to grow together as members of the same plant community. A similar, and often more pronounced, stratification is to be found in the underground parts of the different members of a plant community. Thus the root systems of different species of plants, the shoot systems of which appear to be growing in close association with each other, frequently occupy and absorb water from different layers of soil. Plant communities may thus be regarded as definite entities; they have their characteristic composition as regards the species which they contain, and they each have their own definite structure. They are the units which together make up the vegetation of the earth. Plant communities have often been likened to individual organisms because of these features; we shall see later that this likeness is further borne out by the fact that they have developmental histories.

Ecological Factors

We have seen that vegetation is, so to speak, composed of a mosaic of plant communities. In a country like Britain these communities are varied in character and are often markedly different from each other in both composition and structure. These differences that exist between plant communities can often be connected in a general way with obvious environmental conditions. For example, we expect the vegetation of a marsh along the banks of a sluggish river to differ from that of a heath on a dry sandy hill. Or again, we understand to some extent the occurrence of beech woods on the chalky soil of the Downs, and the presence of oak woods on the non-calcareous slopes of the Lake District hills. In the case of the marsh and the heath the differences between the communities appear to be largely due to differences between the amounts of water in the respective soils, while on the other hand the presence of beech forest or of oak forest would in many places appear to be due to the composition of the underlying rock. Again, the vegetation of a mountain-top differs from that of the slopes a thousand or more feet lower down, a fact which can be readily related to the difference between the climatic conditions prevailing in these two situations. From these examples it is clear that dissimilarities between plant communities may be due to various causes, a few of which are, the amount of soil water, the nature of the underlying rock so far as it affects the composition of the soil, and local climatic conditions. It is obviously useless to attempt to explain the vegetation of a region solely on the basis of any one of these causes, as a little thought will make it clear that they all, and many more, may collectively operate to give rise to a particular type of vegetation.

These various conditions which affect the growth of plants and determine the nature of plant communities are termed *ecological* or *habitat factors*. The word habitat was originally used by field botanists merely to denote the particular situation in which a plant was found growing; its meaning as an ecological term is now much wider, embracing, as it does, the whole of the environmental conditions under which a plant or a plant community exists. In other words, the habitat includes the sum total of the ecological factors which are operating on the plant or plant community.

Habitat factors can be grouped under three headings, namely, *climatic factors*, which have origin in the climate of the region where the vegetation is situated; *physiographic factors*, which include those resulting from topography and from soil or *edaphic* conditions; and *biotic factors*, which are the various effects resulting from the vital activities of animals, including man, and of the plants themselves. It will be readily understood that these various factors are to a considerable extent interdependent one upon another. For instance, to take the example already quoted of the difference between the vegetation of a mountain summit and that of the slopes below, here the differences in plant communities may be largely due to climatic differences, but these climatic differences are in turn due to topographic causes. Similarly man may bring about changes in vegetation by cultivating the soil and so altering the edaphic factors operating.

The problems relating to habitat factors are the most important ones that occupy the attention of the ecologist. Many of them are extremely complex and the difficulties attending their satisfactory solution may be very great. Nevertheless, it is on the investigation of the nature of, and the determination of the effects of different habitat factors that the student of ecology should concentrate most of his attention, for in this direction lie the only real advances in the subject.

CLIMATIC FACTORS

The climatic factors of the habitat are rainfall, atmospheric humidity, wind, temperature, and light. The behaviour of these factors in any given region as regards their individual intensity and duration of action, and the seasonal distribution of this behaviour, constitute the climate of the region. Certain more or less definite combinations of these conditions relating to factor behaviour are recognized as characterizing definite types of climate, and a particular type of climate prevailing over a region tends to produce, in that region, a definite predominant or, as it is termed, *climax* type of vegetation (see p. 50). Thus, over much of western Europe, the climate is such as results in deciduous forest occurring as the natural climax vegetation. Where this climax type does not occur its non-occurrence is found to be due to a predominating local operation of some powerful habitat factor. The most important influences which modify the climatic climax type of vegetation or prevent its development, are soil (edaphic) factors and biotic factors. The latter are, in the majority of cases, the outcome of human activities, the effects of which are clear in any region where farming operations are carried on.

Of the climatic factors enumerated above each one individually contributes to the general effect of climate by influencing the life processes of the plant species which make up the vegetation. Atmospheric humidity, wind, and light influence directly the activities of the aerial parts of plants, while temperature affects the vital processes of both aerial and underground organs. Rainfall operates indirectly through the medium of other habitat factors, its chief importance being naturally connected with its influence on the available soil water, a matter which will be discussed when dealing with edaphic factors; rain is also important in regard to its effect on atmospheric humidity.

Atmospheric humidity is important chiefly because of its influence on the rate at which plants lose water through transpiration from their leaves. Its intensity as a habitat factor is chiefly influenced by temperature. The rate of transpiration is governed to a great extent by the same conditions as those which affect the rate at which simple evaporation of water takes place. This is dependent not so much on the absolute amount of water vapour present in the atmosphere, as on the amount of water which it is able to take up before becoming saturated, or, in other words, its *saturation deficit*. Saturation deficit bears a direct relationship to temperature, as the higher the temperature the more water vapour is the air capable of holding. This fact is well illustrated by the deposition of water from the air in the form of dew when the temperature falls at night after a dry summer day. Information regarding the saturation deficit of the air is usually obtained by ascertaining what is known as its *relative humidity*; this is the amount of water vapour present in the air, expressed as a percentage of the total amount of water vapour required to saturate it at the particular temperature prevailing at the time of the determination. A low relative humidity therefore means a high evaporation rate. This condition of the atmosphere which governs the rate of transpiration, besides being affected by purely climatic and geographical causes, is affected by the plants themselves. These by their transpiration tend to raise the amount of water vapour present in the air immediately surrounding them. The degree to which this effective increase in humidity is brought about by plants depends on whether the air is still or moving. Wind tends to increase transpiration by bringing about the removal of the moisture-laden air from around the stomata of the transpiring plants, and its replacement by drier air. Here again the biotic effect of the plants themselves may be important in so far as close-growing vegetation reduces the velocity of the wind and so tends to reduce transpiration.

It will be clear in view of the great physiological importance of transpiration that a factor like atmospheric humidity, which so directly affects this process, must play a considerable part in determining what plant species are able to exist in any given situation. For example, the highly humid air within a lowland oak forest or in a sheltered mountain gorge, is largely responsible for the delicate and obviously moisture-loving or hygrophilous character of many of the plants to be found there. At the same time, when considering the effects of atmospheric humidity on vegetation, its dependence on other factors must be continually kept in mind.

Wind.—The action of wind as an ecological factor may be direct or indirect. The direct effect of wind is seldom to be seen in any marked degree in this country. On exposed mountain-tops such as for example in Wales or the Lake District, plants frequently live in danger of being uprooted and blown away by strong winds, with the result that in these situations, the vegetation is largely composed of species which have a prostrate habit of growth and a tenacious underground root or rhizome system. Apart from such cases one may take into account occasional gales which sweep the country and cause considerable mechanical damage to trees and other plant life ; these are, however, insufficiently prevalent to play any important part in the moulding of vegetational features.

Of much greater significance are the indirect effects of wind. The chief of these is its influence on the rate of transpiration of plants, a point which has already been briefly mentioned. Air currents, by sweeping away the layers of moist air from the stomata-bearing surfaces of leaves, tend to increase transpiration. Wind velocity increases with height above the surface of the soil so that the nearer the foliage of a plant is to the ground, the less will be the danger of its undergoing excessive transpiration due to wind action. This effect is indicated by the stunted character of trees growing in exposed situations. In connexion with the height to which plants grow under different conditions of exposure, it is important to remember that a balance has to be established in regard to water relations. A plant cannot continue to exist under conditions where loss of water by evaporation from its leaves, is greater than gain in water by absorption from the soil. On account of the fact that evaporation rate due to wind action tends to increase with increased height above the soil, there is a limit to the height to which any particular plant may grow with safety in any given situation. Thus the height of a tree may be limited by the dying off of those of its upper shoots which grow up above the level where transpiration becomes excessive. Here again the biotic effect of mutual protection becomes evident, as the trees in a wood growing in a situation exposed to strong winds are taller than isolated trees growing under otherwise similar conditions, and the trees along the edge of the wood on the windward side are not so tall as those which form the rest of the wood (see Fig. 1). A further example of this same effect is shown in a great many plant communities in which all the taller plants grow to a practically uniform height or ‘ general vegetation level ’ as it has been termed. This is largely due to the fact that any single plant growing above this level has its upper parts exposed to a greatly increased wind action with the result that their growth is usually inhibited by desiccation. The asymmetrical growth form of isolated trees in exposed situations is due for the greater part to death from excessive transpiration of many or all of the shoots that grow out on the windward side; in addition to this, however, there is usually to be seen a certain amount of actual bending of branches towards the leeward side, as a result of the direct mechanical effect of wind pressure. As a further instance of the interdependence of ecological factors one upon another it may be pointed out that as wind affects plants chiefly through the medium of transpiration, its action will be modified very considerably by the rate at which absorption of water from the soil can take place. This latter will naturally depend upon such factors as soil temperature and various other edaphic conditions. Temperature may be extremely important, as wind action may be exceptionally severe at times when soil conditions are so cold as almost or entirely to arrest absorption of water by roots.

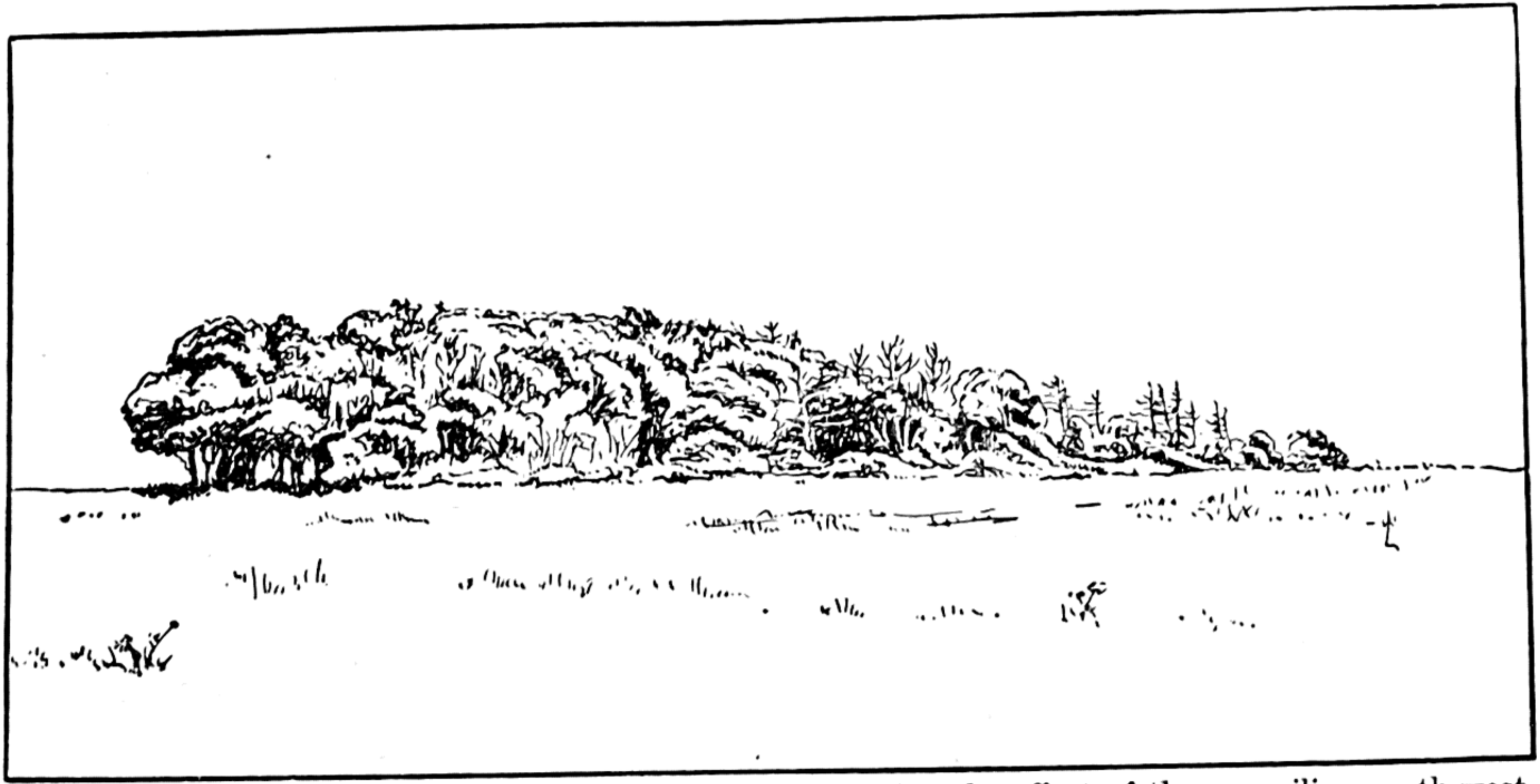

FIG. 1.—Sketch of a small wood on the Dorset coast showing the effect of the prevailing south-west winds (windward side to right of sketch)

For further explanation see text

While many plants are very sensitive to exposure and are unable to exist in places where this exceeds relatively moderate limits, others exhibit a remarkable degree of adaptability to varying conditions. A case in point is that of the bilberry (*Vaccinium Myrtillus*) which in sheltered situations may form comparatively large shrubs two or three feet high, while on exposed mountain-tops it consists chiefly of an extensive underground rhizome and root system with a stunted development of aerial shoots which often do not project more than an inch above the surface of the soil.

Temperature as an ecological factor is more general and uniform in its operation than atmospheric humidity and wind. It shows only slight effective variation, so far as its average value is concerned, over areas of restricted extent such as Great Britain. On the other hand, if we consider the vegetation of the earth as a whole, or even of a continent like Europe or America, we find it possible to correlate to some extent certain vegetation characters with annual or with seasonal temperature. As we have already seen, the question of temperature enters into any consideration of the action of wind and atmospheric humidity, indeed, from our point of view, temperature is best treated not as a separate habitat factor, but in relation to other factors which are more definite and particular in their operation.

When studying vegetation in this country we find that although the general characters of the plant communities present are not related definitely to temperature as a habitat factor, the individual species present in these communities appear to be, to some extent, determined by it; so that we find plants growing in the south of England which do not occur in the more northern parts of the country. In some cases this may be due to limitations of temperature operating through, for example, the ability of certain species to withstand freezing; on the other hand, much of this restricted distribution of species may be due to the fact that they are relatively recent arrivals in the country and have not yet had time to spread beyond the areas they occupy at present. In view of the universal importance of the effects of temperature on all the vital processes of plants, it must be continually kept in mind when considering other ecological factors and their influence on vegetation.

Light.—Owing to the great physiological importance of this factor in the metabolism of plants, one would naturally tend to consider it to be of equal significance as an ecological factor. Its interest to the ecologist, however, is not so great as its physiological importance would suggest, on account of the fact that its action is comparatively uniform over wide areas. The general features of plant communities are not affected by light, except in the case of small communities growing in deeply shaded situations such as caves, etc. ; it is only the subordinate species within the plant communities, which determine what we may call their internal structure, that show modifications in relation to the operation of this factor. The majority of plants have definite requirements in regard to light. Some will only thrive if they receive a full unrestricted amount of sunlight, others favour a moderate amount of shade, while others can stand deep shade. On the other hand, there are plants which exhibit a considerable range of adaptability, apparently being equally at home in both fully lighted situations and in shade. As an example of the latter we have the ubiquitous bracken (*Pteridium aquilinum*). Shade conditions are mostly brought about by plants themselves. Forest trees produce the shade conditions under which the undergrowth vegetation exists. The amount of shade cast by different types of woodland also varies greatly. As an example of this variation we might compare the very considerable ground flora of an oak wood with the almost entire absence of undergrowth that is met with in the deep shade of some beech, and pine woods.

When investigating the importance of light as a factor in the determination of the structure of plant communities, we are faced with the difficulty of separating the effects due to light intensity from those arising from the operation of other factors. The most important of these other factors is atmospheric humidity. Shade conditions are almost invariably accompanied by increased atmospheric humidity, as compared with conditions of full light. Differences in temperature and intensity of wind action also in the same way accompany differences in light intensity. Plants grown under shade conditions often show certain characteristics of anatomical structure, more particularly in their leaves, which distinguish them from plants grown in full light. It must be noted, however, that many of these structural peculiarities are also to be found in the same plants when grown in full light but in a moisture-saturated atmosphere.

Physiographic Factors

The physiographic factors of the habitat are those which have origin in the form, behaviour and structure of the earth's surface. Irregularities in the form of the earth's surface result in mountains, hills, valleys, and all the related conditions which give rise to a group of factors which we may term topographic factors. The behaviour of the earth's surface includes such processes as erosion, the silting up of lakes and river-mouths and the accumulation of sand and shingle along the sea coast. These processes are also all mainly due to topographic causes. The structure of the earth's surface includes both the geological features of the rocks forming it and the physical, chemical and biological characters of the soil which largely originates from these rocks. These latter constitute the *edaphic* factors of the habitat; they are of great importance and, in fact, are often treated as a separate group distinct from other physiographic factors.

It must be admitted that modern work on soil shows, as we shall see later, that biotic and climatic conditions are often of far more importance in the determination of soil characters than such physiographic features as the geological nature of the underlying rock. This latter, however, does largely affect the soil; it also frequently plays a prominent part in the determination of topographic features.

Topographic Factors.—Topography affects the growth of plants in two ways. In the first place it brings about local variations in climatic conditions, and in the second place it modifies the edaphic factors of the habitat.

Climatic effects are best observed in mountainous regions such as Wales or the Lake District. The zones of vegetation passed through as we ascend a mountain usually correspond closely with the changes in climatic factors which accompany increase in altitude above the sea-level. The lowest zone of natural vegetation in either of the localities mentioned is mostly oak forest; it is only here and there, however, that this forest zone now exists, human interference having resulted in its replacement by farm land or by bracken. However, we can still find oak (*Quercus sessiliflora*) forest clothing the mountain-sides up to an altitude of about 1,800 feet in a few places, elsewhere we usually find bracken covering the slopes and occupying the sites of original woodland. Near the 1,500-feet contour climatic conditions are such that the oak trees are no longer able to thrive. Here the trees are stunted and grow as sparse scrub often associated with hawthorn (*Crataegus Oxyacantha*). Above the scrub the vegetation is usually dominated by ling (*Calluna vulgaris*), and this in turn, owing to climatic changes, gives place at an altitude of about 2,000 feet, to more resistant species such as bilberry (*Vaccinium Myrtillus*) and crowberry (*Em-*

petrum nigrum). This change in climate with increasing altitude is due to a number of causes. In the first place the temperature of the air is lower the higher we go above sea-level. Further, owing to increased rarefaction of the air at high altitudes, although a greater amount of radiant energy from the sun reaches the soil on clear days on a mountain-top than in the valley below, radiation of heat from the soil at night is more rapid and the net result is a colder soil. Wind action increases with altitude, and is consequently an important factor on exposed uplands. Greater and more frequent variations in atmospheric humidity occur on mountain-tops than at lower altitudes. The summits and upper slopes may be at one time enveloped in cloud, and under conditions of high atmospheric humidity and frequent heavy rainfall, while at another time, in clear weather, extreme dryness may prevail. Further, much greater extremes between summer and winter climatic conditions are experienced by plants on mountains than by those growing in more sheltered situations down below.

Another topographical cause of local variations in the habitat factors at work on an area, is the slope of the ground. This affects the vegetation by affecting insolation and by affecting the stability of the soil, and the movement of water in it or over its surface.

The effect of slope on insolation is clearly illustrated in Fig. 2. It will be seen that the steepness of the slope and the direction which it faces, determine the area over which a given amount of direct radiant energy from the sun is spread. A soil surface, the plane of which is at right angles to the path of the direct rays from the sun will receive the maximum amount of energy per unit area, deviations from this angle result in a reduction in the amount of direct sunlight received per unit area. This slope effect is of considerable importance in practical agriculture and horticulture. Its influence on natural vegetation can be clearly seen if the compositions of the plant communities on the north side of a mountain be examined and compared with those on the south side. The vegetation of the north-facing slope will be found to contain a greater abundance of shade-loving species and a richer bryophyte flora, and to be, on the whole, less xerophilous than that of the south-facing slope.

Slope may play an important part in determining the character of the soil. There is always a tendency for water movements to remove soil from a slope, and to carry it down and deposit it in a valley, or where the slope is less steep (see Fig. 3). Further, where the plane of a slope cuts across rock strata, erosion usually takes place more readily than where the strata lie parallel to that plane. This is especially noticeable if the rock is of a shaly, friable nature. If the slope is steep this may result in a soil surface of unstable material on which vegetation is unable to establish itself, or is only just able to maintain a precarious foothold. In addition to this we have the effect of slope on the water content of the soil.

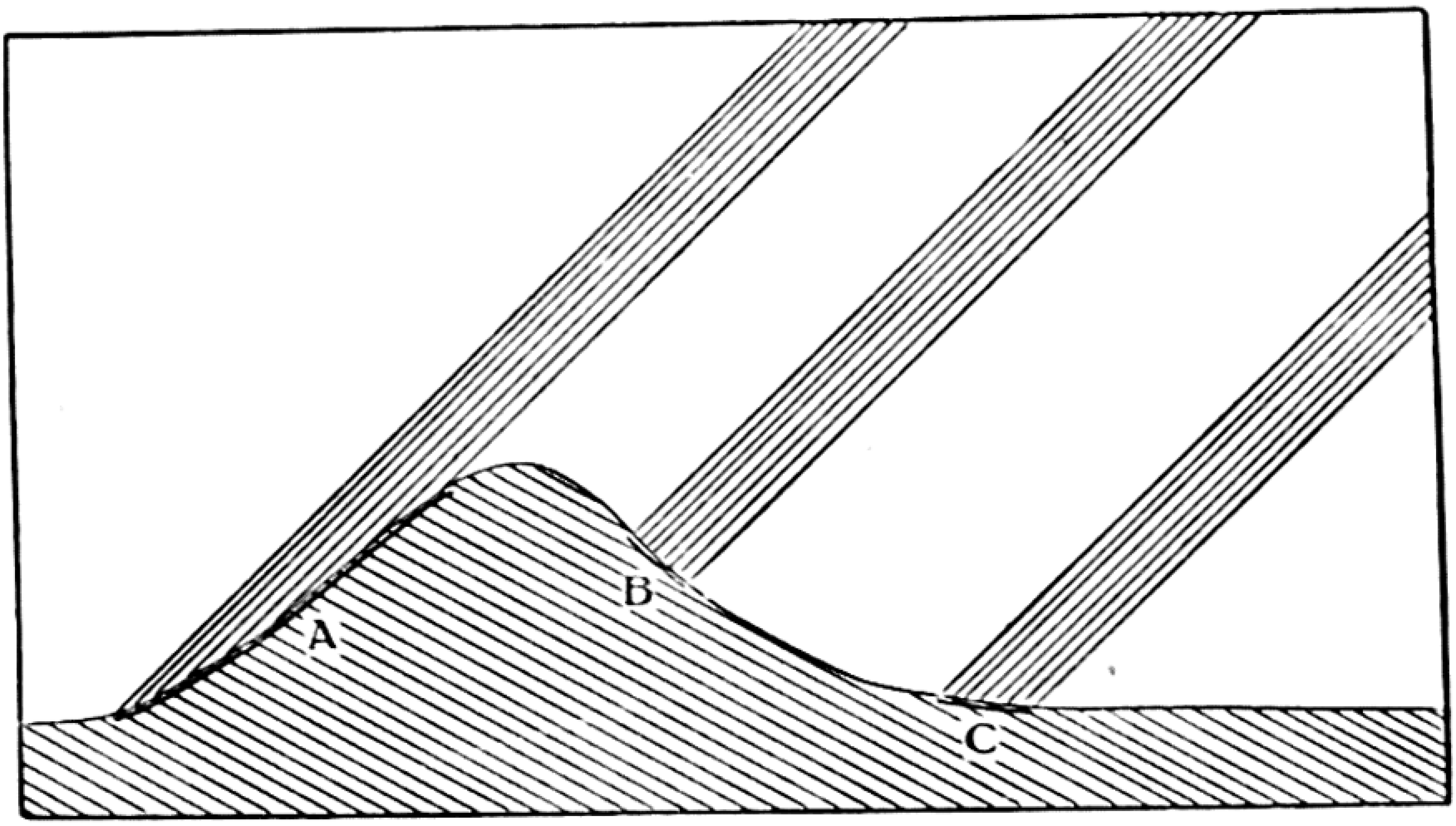

FIG. 2.—Diagram showing how slope affects the area over which three equal beams of light are distributed at A, B and C respectively

A sloping soil surface is usually drier than a horizontal one, owing to the fact that rain-water tends to run off before it has had time to be absorbed. The angle affects the amount of water that runs off in this way, and on steep slopes in regions of high rainfall, active erosion and denudation due to this moving surface water may result in an almost entire absence of higher plants from considerable areas on hill-sides.

Another way in which topography may influence soil conditions is by affecting the position of the water table, that is, the level below which the soil is completely waterlogged. In general the water table tends to be nearer the surface of the soil in valleys than on hills, although modifications of this condition may occur as a result of certain geological causes. This topographical distribution of the water table has important ecological effects in hilly regions where the rock is of a porous sandy character. On the hills, where the water table is deeply situated, owing to the rapid percolation of water downwards through the soil, conditions of drought may prevail. In the valleys, however, in spite of the extreme porosity of the soil, the proximity of the water table to its surface usually results in an ample water supply for plant growth. This effect is illustrated in Fig. 3.

A further erosion and denudation effect is the deposition of material carried by water or wind, which results in the formation of new soil surfaces for colonization by plants. Rivers carry silt down to their mouths and there deposit it as mud flats, or the tide may deposit similar mud flats within a sheltered estuary, and on these, salt marshes may develop, as, for example, at the mouth of the Dovey in Wales, and at numerous other river-mouths along our coasts. Alluvial deposits also occur where streams enter lakes, and on these we find various types of marsh vegetation.

Wind-blown sand along the sea coast accumulates as sand-dunes on which develop vegetation composed largely of marram grass (*Ammophila arenaria*), a plant which, by means of creeping underground stem and root systems, is able to establish itself on the loose sand and eventually bind it together and render it suitable for other species which require a more stable soil.

EDAPHIC FACTORS.—THE SOIL

While climatic factors are of supreme importance in determining the general characters of vegetation over wide areas, edaphic or soil factors are mainly responsible for the more local differences between plant communities to be found within the great climatic regions. From the earliest times the importance of the nature and condition of the soil has been recognized in relation to agriculture and vegetation. Of late years with the advance of the scientific study of agriculture, the necessity of investigating soil problems on intensive lines has become more and more evident, with the result that soil study now ranks as an independent branch of science and as

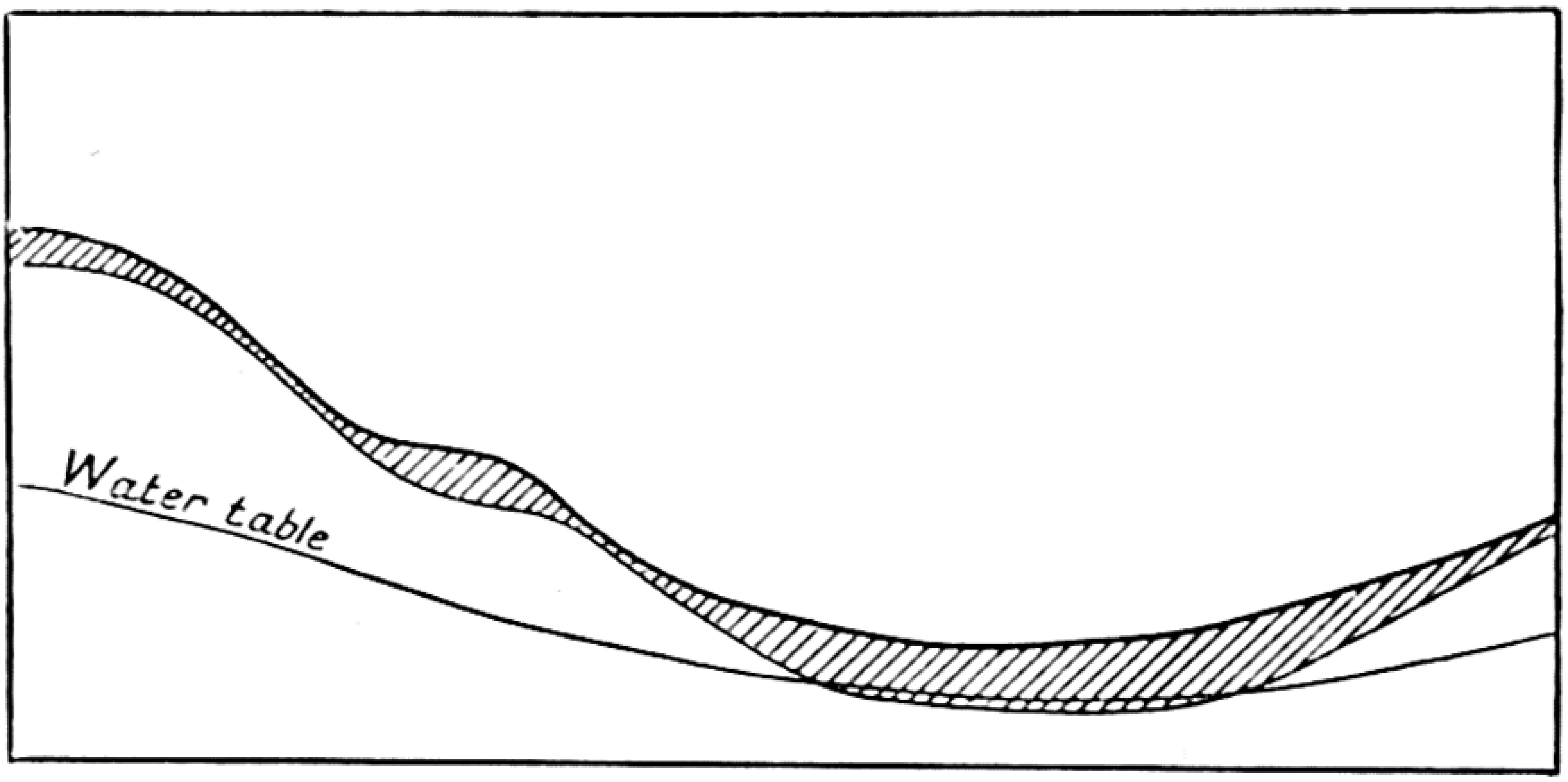

FIG. 3.—Diagram showing variations in the depth of the soil and the position of the water table in relation to topography

The soil is indicated by shading. For further description see text such is called *Pedology.* Although the beginner in ecology will not find it essential to go into all branches of soil science, certain aspects of it will of necessity concern him, and as his work advances he will in various directions recognize the desirability of making a closer acquaintance with pedology. It is proposed here, while dealing with edaphic factors, very briefly to touch upon those pedological matters that are of particular interest to the student of British ecology.

Although the meaning of the term soil is in a general way clearly understood, a definition of soil that can be invariably accepted by the ecologist is difficult to arrive at. We may take the soil as being the whole or part, as the case may be, of the superficial unconsolidated layer of the earth's crust, its limits as regards depth being determined by whether or not it directly or indirectly affects the activities of the plants growing at the surface.

The four essential constituents of the soil are: (*a*) mineral matter consisting of fragments of various sizes resulting from the disintegration of rock by the natural processes known as weathering, (*b*) organic matter, arising from the death of plants and parts of plants growing in or on the surface of the soil, or artificially added as manure, (*c*) soil water containing dissolved substances, and (*d*) soil air. Local quantitative and qualitative variations in these constituents affect the plants which grow in the soil and constitute what we call edaphic factors.

The Mineral Matter of the Soil.—Variations in the sizes of the particles which form the mineral constituent of the soil operate on vegetation, for the greater part indirectly, by bringing about variations in the soil water and the soil air. The amount of water which is available for absorption by plants growing in the soil is determined to a considerable extent by what is known as the *mechanical composition* of the soil, that is, the relative proportions of the different-sized mineral particles present in it; available water is, as we have already seen on page 20, also affected by topographical causes. The mechanical composition is determined by a laboratory process known as mechanical analysis (see p. 69) whereby the mineral part of the soil is separated into a number of arbitrary fractions each consisting of particles whose size lies between definite limits. These limits have been fixed for the sake of convenience and uniformity by the International Society of Soil Science and are given below :

Diameter of Particles	*Designation*
2·0–0·2 mm.	Coarse sand.
0·2–0·02 mm.	Fine sand.
0·02–0·002 mm.	Silt.
Less than 0·002 mm.	Clay.

The importance of the mechanical composition of the soil lies in the fact that these various categories of particles carry with them definite soil properties. Every one is familiar with the differences that exist, for the gardener, between a sandy soil and a clay soil. The former is spoken of as being light, it is loose, easy to work, porous and tends to become dry quickly, whereas a clay soil is heavy, is not porous, is sticky when wet and tends to become hard and consolidated when dry, and is very retentive of water. These differences are due in the main to the respective proportions of large and small particles in the two soils. In the sandy soil the larger particles predominate, while in the clay soil the smaller particles are in preponderance. In order to arrive at a clearer understanding of the relations existing between different mechanical soil types and the vegetation they support, it will be advantageous to consider the specific properties of the individual constituents.

Coarse Sand.—The larger particles of the soil include the stones, gravel, and the coarse sand ; the first two of these consist of fragments of unaltered rock. In the case of coarse sand the particles are, in British soils, usually almost entirely composed of quartz, they are insoluble in water and are chemically inert. The properties they convey to the soil are due to the fact that they are relatively large and irregular in shape, the result being that the spaces between them are large and so allow movements of air and water to take place with very little hindrance. Thus coarse sand in the soil tends to aid good aeration and rapid drainage with the consequent ready removal of soluble substances by the process known as leaching. It is therefore clear that although good soil aeration is advantageous to plant life, excessive drainage arising from a superabundance of these large particles may tend to result in soil conditions which are unfavourable to plant life on account of deficiency in available water and dissolved mineral substances. Exceptions to this state of affairs may, however, occur, as has been pointed out on page 20.

Fine Sand.—In the case of fine sand the attendant relations to soil air and soil water are very similar to those described in connexion with coarse sand, except that the smaller size of the particles renders these relations less extreme. Fine sand, however, differs from coarse sand in that a slight admixture of particles of still smaller size causes it to cohere and cake when dry.

Silt.—Silt, like coarse and fine sand, may be taken as being composed of fragments of rock-forming minerals. The smallness of the particles of this soil fraction causes it strongly to retard movements of air and water. Silt also exhibits the properties of colloids to a slight extent as, for example, in that it has a slight tendency to absorb and retain water. Fine sand, although the smallness of its pores may only allow water to move through it slowly, nevertheless does not actually absorb an appreciable amount of water. Finer silts, when wet, form heavy stiff soils which are difficult to work, but which, unlike clay soils, when dry are easily crumbled.

Clay.—Clay differs very markedly both chemically and physically from the three soil constituents described above. In the first place clay may in some measure be secondary in origin, not being entirely composed of particles of rock-forming minerals. Such particles of secondary origin are formed by precipitation from solutions of products of the chemical weathering of rock constituents, that is, their decomposition by water, often aided by dissolved carbon dioxide and organic acids. Clay, owing to the smallness of its particles, is colloidal in nature and, like other colloids such as gelatin, is able to take up and retain considerable quantities of water, and as it takes up water it increases markedly in volume. In the presence of small quantities of electrolytes clay particles show colloidal behaviour in that they may become aggregated together to form what are virtually larger particles, or *crumbs* as they are termed, so that the clay is said to be *flocculated*. This phenomenon of flocculation can easily be demonstrated by preparing a suspension of clay in water and dividing it into two portions ; if a small quantity of a solution of a salt such as calcium chloride be added to one portion of the suspension and both allowed to stand, it will be noted that the particles of the suspension to which the electrolyte was added, quickly settle, leaving a clear liquid above, whereas the untreated suspension continues indefinitely to remain turbid. On the other hand, many salts and alkaline hydroxides, like sodium hydroxide, have a reverse effect in that they cause compound aggregates of clay particles to disperse into their individual components, a process known as *deflocculation*. The flocculating effect of lime on clay has long been known to agriculturalists, but the whole question is extremely complex and for further information regarding it the student is referred to those works which specially deal with soil problems. This property of clay has an important bearing on the relationships between plants and soil, in that flocculation increases the permeability of clay to air and water. Deflocculated clay is very sticky when wet and is extremely impermeable to water.

Clay differs from the practically inert sand and silt fractions of the soil in that it is chemically reactive, and so is important in connexion with the supply of soluble mineral salts in the soil water.

The Organic Matter in the Soil.—Organic matter derived mostly from the dead remains of plants forms one of the most important constituents of the soil. Although organic matter is always present, the amount occurring in different soils varies between a mere trace in certain examples to a figure approaching 100 per cent. in pure peat. The organic matter is the seat of the activities of soil micro-organisms and, as is well known, these activities are of vital significance in connexion with the supply of nitrogen required by higher plants.

Soil organic matter is extremely important on account of its water-holding properties; thus soils with low organic matter content, unless they contain a large proportion of clay, quickly lose their water and become dry, and this rapid loss of water, as we have seen, is accompanied by a leaching away of soluble salts.

Dead plant remains when added to the soil are immediately attacked by micro-organisms which bring about their decay, so that they gradually pass from that state in which the original plant structures can be recognized, to a condition in which they appear as a dark-coloured amorphous and relatively inert substance which is termed *humus*. Humus is thus that part of the soil organic matter which has become structurally unrecognizable, it is colloidal in character and together with clay forms what is pedologically referred to as the *colloidal complex* of the soil.

Under natural conditions much the greater part of soil organic matter is derived from the dead remains of plants growing at its surface. These dead plant remains suffer one of two fates; they are either completely oxidized by bacteria to simple inorganic compounds, the chief of which are carbon dioxide and water, by the process known as oxidative decomposition, or they are converted into humus by processes referred to as *humification*. The relative degree in which these two actions take place varies according to the climatic and other conditions prevailing where the soil-forming processes are going on. Oxidative decomposition is most active at temperatures of 35° to 40° C. and under conditions of good soil aeration, moderate soil moisture and a source of available calcium such as the presence of calcium carbonate in the soil. The carbon dioxide produced in the soil in this way is very important in connexion with soil-forming processes largely on account of its solvent action when dissolved in the soil water.

The reduction of one or more of the conditions mentioned above as favouring complete oxidation of soil organic matter leads to increase in the process of humification. Conditions under which there is complete or almost complete absence of oxygen, or as they are termed, anaerobic conditions, such as exist in water-logged soils, favour humification even when other circumstances may be suitable for complete decay. For example, in fens and shallow lakes where temperature and calcium supply are suitable for oxidative decomposition, humification proceeds and the accumulation of what is known as fen peat or neutral humus takes place.

Under conditions of anaerobiosis due to water-logging, and of shortage of calcium or other bases in the soil, humification results in the formation of acid peat. Acid peat or acid humus is characterized, as its name implies, by having a markedly acid reaction, by being poor in bases, and by the fact that it decomposes slowly and contains a larger or smaller amount of plant remains with their structure preserved. Such acid peat in Great Britain reaches its greatest development in regions where the soil-forming rocks are non-calcareous and where climatic conditions are for the most part wet and cold, as, for example, in many parts of Scotland and in England on the Pennines and Dartmoor.

Humification also may proceed under relatively dry conditions where there is a shortage of calcium and other bases as, for example, in soils formed on sand and acidic rocks. Such peat layers, which are pronouncedly acid, are usually only a few inches in thickness and are comparatively dry. They are formed in various parts of the country under heath or pine wood vegetation. Heath plants and pines absorb only small quantities of bases from the soil and consequently their discarded foliage, which accumulates as organic matter, is poor in bases and is not readily acted upon by soil bacteria.

It will be gathered from the foregoing that the rate of formation of humus, and similarly the rate of oxidative decomposition taking place in a given soil, is dependent upon the state of balance existing between the two sets of conditions which favour these respective processes. As all degrees of this balance occur, so we find the quantity and kind of humus present in soils showing considerable variations in different habitats.

In the majority of situations in Great Britain where humification is actively taking place, it is doing so under conditions of shortage of calcium and other bases. The consequence is that the resulting humus is usually markedly acid in reaction, in fact, natural British soils are, on the whole, acid. This is, moreover, frequently the case even at the surface of soils which overlie rocks of a calcareous nature, the reason being that the calcium carbonate has been removed from the upper layers by the leaching action of percolating water containing dissolved carbon dioxide.

Soil Acidity.—Owing to the fact that a large number of plant species appear to show a distinct preference for soils whose acidity lies between definite limits, soil acidity has received a considerable amount of attention from ecologists.

Measurements of soil acidity are carried out by determining the hydrogen ion concentration of a suspension of the soil in distilled water, hydrogen ion concentration being a measure of the degree of acidity. For convenience of expression the actual hydrogen ion concentration, that is, the number of free hydrogen ions present in a litre of suspension, is not used; instead, a number indicating the logarithm of the reciprocal of the hydrogen ion concentration, termed the *p*H value, is taken. This mode of expression of acidity depends upon the theory of electrolytic dissociation which states that water and aqueous solutions contain free positively charged hydrogen (H +) ions and negatively charged hydroxyl (OH −) ions. Also at a temperature of 18° C. the total number of free hydrogen ions and hydroxyl ions together is constant, being always $10^{-14 \cdot 14}$. When the number of free hydrogen ions equals the number of free hydroxyl ions, the solution is neutral; if hydrogen ions are in excess, the solution is acid; if hydroxyl ions are in excess, the solution is alkaline. The degree of acidity or alkalinity, therefore, depends upon the relative numbers present of these respective free ions. Thus, one litre of neutral distilled water contains $10^{-7 \cdot 07}$ free hydrogen ions, whereas decinormal hydrochloric acid contains $10^{-1 \cdot 04}$ and decinormal sodium hydroxide, $10^{-13 \cdot 07}$. If, then, the reactions of these liquids are expressed in terms of *p*H, the *p*H value of the distilled water is 7·07, that of the N/10 hydrochloric acid is 1·04 and that of the N/10 sodium hydroxide is 13·07.

Actual determinations of soil reaction are conducted in the field colorimetrically with a fair degree of accuracy by adding certain dyes, which change colour between definite ranges of *p*H, to the soil suspension to be tested; the method will be described in more detail in a later section (see p. 72). For more accurate estimations of *p*H the laboratory method of electrometric measurement must be carried out (see Russell, 1932, p. 568).

When studying the distribution of plants in the field in relation to soil conditions, one finds that certain species nearly always occur on soils which show a markedly acid reaction; examples of such species are *Rumex acetosella*, *Calluna vulgaris*, *Nardus stricta* and many others. Owing to the fact that such acid soils are always deficient in calcium, these plants are frequently referred to as *calcifuge* species. On the other hand, there are plants like *Mercurialis perennis* and *Agrostis alba* which appear to be intolerant of acid soil conditions; such species are termed *calcicole* or lime-loving species. Actually, when careful examination is made of the preferences of various plants in regard to soil reaction, it is found that a whole range of differences in behaviour exists. This point is brought out in Table I taken from an account, published by Olsen, of researches carried out on the problem in Denmark.

It is pointed out by Russell (1932) that plants can be divided into three groups according to their behaviour towards soil reaction, namely:

(1) 'Those tolerating only small variations in soil reaction, the optimum being at or about the neutral zone or on the alkaline side.

(2) Those tolerating only small variations in soil reaction, the optimum being on the acid side.

(3) Those tolerating considerable variation in soil reaction.'

The species given in Table I will be found to fall naturally into these three groups.

There are considerable differences of opinion regarding the question as to how soil reaction actually influences plants. One supported by Olsen (1936) is that plants in acid soils absorb appreciable amounts of manganese. Some species are immune to the toxic effect of this element while others are not. Another

TABLE I

Average Frequency of Plants on soils of lifferent *p*H

(*From* Olsen, 1923)

	*p*H Classes								
	3·5–3·9	4·0–4·4	4·5–4·9	5·0–5·4	5·5–5·9	6·0–6·4	6·5–6·9	7·0–7·4	7·5–7·9
Deschampsia flexuosa	86	68	40	—	—	—	—	—	—
Molinia caerulea	94	84	46	13	—	50	40	30	—
Potentilla erecta	67	99	63	73	48	45	10	20	—
Calluna vulgaris	20	47	10	20	—	—	—	—	—
Agrostis tenuis	30	90	93	70	48	—	—	—	—
Vaccinium oxycoccus	—	70	—	27	23	—	—	—	—
Agrostis canina	—	100	100	73	63	100	—	—	—
Festuca ovina	—	100	47	35	20	20	50	—	—
Anthoxanthum odoratum	33	47	79	80	83	76	27	30	30
Holcus lanatus	—	50	22	77	68	56	74	65	42
Hieracium pilosella	—	—	50	20	27	20	—	—	—
Rumex acetosa	23	30	43	32	48	60	44	50	—
Festuca rubra	—	37	43	71	99	86	96	86	100
Potentilla palustris	—	15	23	41	68	30	20	—	—
Ranunculus acris	—	—	13	53	62	58	51	90	63
Deschampsia caespitosa	—	—	—	40	67	62	33	52	23
Cirsium palustre	—	—	—	33	28	43	24	30	—
Phragmites vulgaris	—	—	—	—	10	45	35	28	33
Spiraea ulmaria	—	—	—	10	10	40	50	30	—
Lathyrus pratensis	—	—	—	—	40	37	55	73	50
Angelica sylvestris	—	—	—	—	—	35	33	48	30
Tussilago farfara	—	—	—	—	—	10	10	55	80
Agrostis alba	—	—	—	—	—	—	30	65	60
Carex hirta	—	—	—	—	—	—	15	15	35

view put forward by Hartwell and Pember in 1918 and widely held in the United States is that in very acid soils, small quantities of soluble aluminium compounds are present which are held to be toxic to calcicole plants. Experimental evidence, however, has shown that aluminium salts are not toxic to all plants which favour alkaline soils. The third possibility which is supported by the work of soil chemists in this country, is that the injurious nature of acid soil conditions to many plants is due to the fact that such conditions are usually associated with calcium shortage. It may be that each of these views is correct for certain particular cases and that owing to the existence of physiological differences between individual plant species, no single and universally applicable explanation of the problem is possible.

With regard to those plants whose distribution is definitely limited to soils of markedly acid type, the solution seems to lie in the fact that such species have a specialized type of metabolism; little is understood regarding this question, though certain suggestions have been put forward relating to it.

Soil acidity is without doubt an important factor in the determination of the distribution of certain plant species; only further research will reveal to us the ultimate physiological details of its actual mode of operation.

The Soil Water.—The water content of the soil is more important than any other ecological factor in causing differences between plant communities, in fact, as we have seen, many other habitat factors affect plants not directly but indirectly by influencing the water content of the soil. Soil water is not only important in connexion with the direct water requirements of plants, it is the medium of conveyance for the salts used in plant nutrition and it is responsible in various ways for most soil-forming processes.

From the direct point of view of the plants growing in the soil, soil water exists under two categories; the *available water* which can be absorbed by plants, and the *non-available water* which cannot be absorbed by plants. The non-available water is that which is usually referred to as the hygroscopic water and is tightly held as thin films surrounding the soil particles, and in association with the soil colloids (see p. 26). Under the heading of non-available water might also be placed most of the so-called gravitational water which is not retained by the soil but which simply drains away into the subsoil and so is lost to plants growing at the surface. The available water consists of two parts, namely, that which is taken up by the soil colloids in the process of swelling and known as *water of imbibition*, and that which is held in the spaces between the non-colloidal soil particles. This latter, when the water content of the soil is low, is believed to be in the form of rings surrounding the points of contact of the particles. Increase in soil moisture causes these rings to run together to form a kind of network of water with continuous air passages running through the meshes. The point at which, as a soil loses water, this free water assumes the form of discontinuous rings is referred to as the *lento-capillary point* and when this point is approached, capillary movements of water within the soil become extremely slow. It has now been experimentally shown that even when the moisture content is above the lento-capillary point, water movement by capillarity is very limited in extent. The height to which water can rise by this means naturally varies with the mechanical composition of the soil, and has been found by Keen (1928) to be as follows:

Coarse sand	35 cm.
Fine sand	70 cm.
Heavy loam	80 cm.

It is interesting to compare these facts with the older view which laid considerable stress on the fact that the spaces between the soil particles acted as capillary tubes and on their capabilities of conducting water, the so-called capillary water, up from the saturated water table below, and in this way supplying the needs of plant roots situated near the surface of the soil.

The term lento-capillary point applies to soils of a homogeneous nature under laboratory conditions. Soils in the field are seldom uniform in composition, so the amount of water present when the lento-capillary point is reached will vary considerably from place to place and at different depths below the surface, or, technically speaking, in different soil *horizons*. Under field conditions then, the mean amount of water present in the soil when capillary movement becomes negligible is termed the *normal moisture capacity*.

This modern conception of the distribution and movement of water in soils is important in relation to the activities of plants. Plant roots can only continue to absorb water from soil beyond their immediate vicinity until the normal moisture capacity of the soil is reached; further adequate water supply can then only be obtained when capillary movement is again made possible by rainfall, or when fresh soil is tapped by the extension of the root systems.

Loss of water by evaporation from the soil is also dependent on these same conditions. Evaporation from the soil surface, the rate of which depends, as in the case of transpiration, upon temperature, wind, and atmospheric humidity, continues actively until the upper layers of the soil have reached the lento-capillary point. Then, owing to the arrest of capillary movement of water towards the surface of the soil, surface evaporation practically ceases. Evaporation within the soil itself, however, continues to take place through the medium of the soil air, the rate of this naturally depending upon the composition and structure of the soil.

A further important point is the rate at which percolation of gravitational water through the soil to the water table below, with its consequent leaching action, takes place. This will naturally depend upon three things, namely, rainfall, the physical properties of the soil, and the rate of evaporation. The ultimate fate of rain-water after it falls on the soil will vary greatly with different soils. In sandy soils percolation will be rapid and most of the water will gravitate to the water table, but in soils containing a high percentage of clay or humus, which only allow of slow water movements, the saturated region may be restricted to the upper layers and much of the rain-water may run off at the surface if the surface is sloping so that the latter in consequence may suffer considerable erosion. On cessation of the rain, evaporation and transpiration again reduce the water content of the upper soil layers so that little, if any, water may reach the water table. From these two examples it will appear evident that the various conditions appertaining to the water relations of soils must be carefully considered in each individual example encountered.

The Soil Air.—The presence of a continuous air system which permeates all but water-logged soils has already been mentioned a number of times, and the importance of this air in connexion with the evaporation of water within the soil has been pointed out. This soil air is essential to the respiratory activities of underground plant organs, and of the soil micro-organisms. The percentage volumetric composition of normal air is 20·96, 79·01 and 0·03 per cent. for oxygen, nitrogen, and carbon dioxide respectively. Russell (1932) states that for arable land the soil air usually contains more than 20·3 per cent. of oxygen while the percentage of nitrogen is about 79, and that of carbon dioxide 0·15–0·65. Grassland soils at Rothamsted show a higher value for carbon dioxide, namely about 1·6 per cent., and a lower value, namely usually about 18·4 per cent. for oxygen; such figures may be taken as typical for climates such as that of Great Britain. The fact that the composition of the soil air differs so slightly from that of atmospheric air indicates that an active gaseous exchange takes place between the two. This gaseous exchange can be adequately accounted for by diffusion, by actual gas movements resulting from changes in pressure of the atmosphere and changes in temperature of the soil, by wind, and by the carrying of dissolved air into the soil by rain-water.

In the case of water-logged soils a very different state of affairs exists; here the aerating processes mentioned above are inoperative, so that oxygen deficiency and carbon dioxide excess may be accompanied by the production of other gases such as hydrogen and marsh gas. The composition of the soil air may thus be an important factor in determining the nature of fen and marsh vegetation.

The Development of Soil.—We have dealt with the various constituents of soil and with the more important chemical, physical and physiological processes which take place in it. These constituents and processes in any given soil area were not always as they are now. We can picture for Great Britain a time in the remote past when the greater part of the country was covered with an ice sheet similar to those covering the polar regions at the present day. As the climate became warmer this ice sheet melted, forming great rivers and lakes, and receded towards the north leaving exposed dry land surfaces composed of either bare rock or of deposits of various kinds such as boulder clay, sand, silt, etc. On these exposed surfaces there gradually developed the soils which cover them at the present time. As organic matter forms one of the most important constituents of soil, the development of soil must have proceeded parallel with, and have been largely dependent on, the development of vegetation which followed the retreat of the ice. Most of the soils of Great Britain have thus a long developmental history behind them ; on the other hand, however, there occur areas where, owing to the activities of man, the whole or part of this original soil has been removed, or again practically reduced to its primary inorganic state. On such areas it is possible to observe some of the early stages of soil development. During this developmental period, upward and downward movements of water due to such causes as evaporation and gravity bring about the transport of various constituents from one soil horizon to another so that the soil assumes a stratified structure which can be seen if a section of it is exposed by digging. Such a section is termed a *soil profile*. The soil profile is now recognized as being extremely important, revealing, as it does, the stage of development reached by the soil, and yielding much information regarding the nature of the soil-forming processes in operation. It is now found to be insufficient when examining the character of a soil merely to dig up and analyse a sample ; on the contrary, it is necessary to expose the whole soil profile, and to examine samples from each successive horizon present in the profile.

The soils in this country in general show three main horizons, namely an upper A (*eluviated*) horizon from which, by the action of percolating water, substances are removed and carried downwards, by the process known as eluviation, to be deposited in a second B (*illuvial*) horizon. Below these two lies the C horizon consisting of the unaltered original substratum. The A and B horizons may each show stratification, the strata being indicated by the signs A_0, A_1, A_2, B_1, B_2, etc.

The character of a soil profile depends primarily on climate ; thus to take a simple example, a cool wet climate means that a large amount of rain-water falls on the soil while, on the other hand, evaporation is slow, therefore the tendency will be for water to move through the soil chiefly in a downward direction. Conversely a comparatively dry warm climate may result in alternate downward and upward movements of soil water of more or less equal importance so that definite eluviated and illuvial horizons may not be developed.

The rate at which soil development takes place, and the course followed in the process, will naturally depend to a great extent on the nature of the original substratum. Where this is a hard rock which weathers slowly, soil formation will be slow as also will be the development of vegetation on its surface. On the other hand, if this substratum is soft rapidly weathering rock, or is a deposit of sand silt or clay, given suitably moist climatic conditions, soil development and vegetation development will be relatively rapid. Again, the chemical nature of the substratum, its physical composition on which the rate of water movement depends, and the depth at which the water table lies beneath the surface, will have important effects on the final type of soil produced.

As an illustration of the way in which soil formation proceeds we may consider a group of soils known as *podsols*, which are to be found extensively developed in the north and west of Great Britain chiefly on rocks and glacial deposits which are poor in bases, and where drainage is good. In this region the deciduous forest vegetation which apparently existed in prehistoric times, has been for the greater part removed by human activities and there is a tendency on neglected areas for heath vegetation to develop. As has already been pointed out (see p. 28), heath vegetation favours the formation of an acid type of humus, a fact which gives rise to a characteristic soil profile development.

The profile details of a well-developed podsol at Goldstone Common in Shropshire have been supplied by Messrs. W. M. Davies and D. Owen and are given below :

A_0	0–6 in.	Leaf mould.
A_1	6–9 in.	Greyish-black humified organic matter containing bleached sand grains.
A_2	9–19 in.	Light grey sand. The sand grains are bleached and the layer has an ashy appearance. This horizon contains numerous pebbles which are notably free from iron-oxide stains.
B_1	19–22¾ in.	Humified organic matter. Harder and more compact than the upper humus layer.
B_2	22¾–23 in.	Deposited cemented iron with a well-defined ferruginous lustre, considerably indurated.
B_3	23–35 in.	Cinnamon-yellow light sand containing numerous stained pebbles. The upper portion of the layer is much more strongly coloured, the intensity gradually decreasing with depth. Considerably indurated.
C	below 35 in.	Pebbly brownish-red or purplish-red laminated loose sandy rock.

Abridged analytical data of the various horizons of this profile are given in Table II.

TABLE II

ANALYTICAL DATA FOR PODSOL PROFILE, GOLDSTONE COMMON, SHROPSHIRE

(Davis and Owen)

Horizon.	Loss on Ignition. Per cent.	Clay. Per cent.	From Analysis of Clay Fractions.		pH.
			SiO_2.	$\frac{SiO_2}{Fe_2O_3 + Al_2O_3}$	
A_0	—	—	—	—	3·86
A_1	25·05	2·7	24·94	4·45	3·70
A_2	3·04	1·3	49·89	4·66	3·13
B_1	15·55	8·8	41·16	1·53	3·73
B_2	2·68	2·2	20·70	1·45	4·75
B_3					
C	1·58	3·3	40·67	2·86	4·75

The complete details of the various processes which result in the formation of a soil profile, such as that described above, are not yet fully understood, but the chief stages are as follows. Under conditions of shortage of calcium and other bases, the heath vegetation produces a surface accumulation of acid organic matter (the A_0 and A_1 horizons). Acid soil water thus causes a deflocculation and consequent mobilization of the humus and clay colloids which are carried down by the percolating water and precipitated in the B horizon, leaving a bleached A_2 horizon above. The humus colloids and clay are precipitated in the B horizon, the first giving the dark B_1 layer, and below this are deposited the iron and aluminium. In sandy soils the iron-cemented layer (B_2) is often very hard and is referred to as iron *pan*, the presence of which may inhibit the growth of planted trees such as pines owing to the inability of their roots to penetrate it.

The effect of these processes is clearly indicated in the various values of the $\frac{SiO_2}{Fe_2O_3 + Al_2O_3}$ ratio $\left(\text{usually designated } \frac{SiO_2}{R_2O_3}\right)$ for the different horizons as shown in Table II. The differences between the values of this ratio for the various A and B horizons and that for the C horizon, show the degree to which movements of silica and sesquioxides of iron and aluminium have taken place during the development of the soil from the original substratum.

Variations in the local climatic and geological conditions result in variations in the extent and nature of the different horizons present in podsolic soils, details of which cannot be gone into here but are to be found in special works dealing with the subject (Russell, 1932 ; Robinson, 1932 ; Ramann, 1928). Under agricultural conditions, tillage operations result in considerable modifications of the soil profile ; also in mountainous regions, erosion frequently removes one or more of the upper horizons so that an abbreviated profile is produced.

Besides the podsols, in Great Britain, the other most extensively developed soils are respectively termed *brown earths*, *meadow soils* and *peat soils*. In addition to these, small areas of other soil types occur in relation to particular local geological conditions.

The brown earths appear to be the natural soils which develop under deciduous forest vegetation. Owing to the relatively high base content of the organic litter produced by this type of vegetation, the reaction of the soil water is never far removed from the neutral point. There is consequently no translocation of humus from the A to the B horizons and leaching out of mineral substances is usually only slight in extent. Earth worms are abundant and bring about a mixing of the soil. In profile, brown earth soils do not show the definite zonation present in podsols. There is an upper layer which is usually about one foot in thickness through which the organic matter is more or less evenly distributed. Below this the organic matter content steadily decreases so that there is a gradual transition as one passes down to the parent material of the C horizon. The brown colour of these soils is due to the presence of free hydrated ferric oxide. The artificial replacement of deciduous forest by conifers, as has been carried out in certain parts of England, is found to result in an impoverishment of the soil which tends to bring about a change from brown earth to podsol.

Meadow soils occur on areas where the water table is near the surface or where impeded drainage results in partial water-logging of the soil. The typical vegetation of these soils, as the name implies, consists of grasses, and in the wetter types approximating to marsh, of sedges and rushes. A characteristic common feature of meadow soils is that the water-logged lower horizon is usually grey in colour with greeny-blue or rusty streaks and mottling, and is known as *gley*. The surface horizon is usually grey loam with an upper peat layer; considerable variations in composition and colour, however, occur in this horizon. Under very moist conditions with almost complete water-logging a thick layer of peat may form above the gley horizon giving a soil type known as a peat podsol.

We have already had occasion to refer to the formation of peat (see p. 27) as a result of continued humification of vegetation remains under anaerobic conditions prevailing in marshes and in cold, excessively moist regions. Such processes result in the development of peat soils, sometimes many feet in thickness, and alkaline, neutral, or acid in reaction according to whether the water supply which led to their formation was rich or poor in dissolved mineral matter.

From the foregoing it will be realized that the edaphic conditions of the habitat form an extremely involved and interrelated complex, and for the greater part cannot be easily separated and treated as individual factors. Most of these conditions are extremely difficult to study effectively either as regards their nature or their effects on plants, and further, many of them are as yet little understood. The very brief account given above should in some degree serve to emphasize the extreme importance of a study of the soil as an aid to the elucidation of vegetation problems.

With regard to the various soil types present in Great Britain, the above must be taken as a very general and very much abridged summary of available information on a subject which is as yet by no means complete. The survey of British soils is at the present time being actively carried out, but it is still far from being finished.

For more detailed information relating to soil problems and classification the reader is referred to standard works on the subject (cf. Russell, 1932 ; Keen, 1931 ; Robinson, 1932 ; Ramann, 1928 ; Comber, 1932).

BIOTIC FACTORS

Biotic factors are so called because they have origin in the activities of living organisms, that is, of plants and animals. They may operate directly or indirectly on the aerial parts of plants or on their underground structures. These direct and indirect effects are complex in an extreme degree. They result from the biotic relationships between the plants themselves which we recognize as together comprising a plant community, between these plants and the animals living in or affecting the plant community, and between the plants and the micro-fauna and micro-flora of the soil. It would be hopeless to attempt to discuss or even mention more than a few of the simpler and more obvious of these factors. In a relatively densely populated area like Great Britain one of the most important groups of biotic factors which have operated on the vegetation for many years has arisen out of man's multifarious activities. Farming largely consists of modifying vegetation in certain definite directions. The intensity or efficiency of farming operations varies between wide limits from one farm to another according to the ability of the farmer. On badly farmed land the vegetation possesses many, what we should call, natural features ; hedges grow tall and tend to spread beyond their prescribed limits, bracken, brambles, gorse and other economically useless or objectionable plants that occur in the wild vegetation of the locality are to be found in the fields. On the other hand, well-farmed land presents a highly artificial appearance. The difference between badly farmed and well-farmed land is merely due to the fact that in the case of the former the biotic factors arising from human interference are less intense than in the case of the latter. Of these human interference factors, the most intense is the actual cultivation of the soil and the growing of food crops. Grazing by domestic animals is a less intense factor than cultivation, but it varies in its intensity with circumstance, and each variation has its effect on the character of the grazed plant community which we call pasture. It is the less intense grazing, that frequently occurs on unfarmed stretches of more or less natural vegetation, that chiefly interests the pure ecologist. Here striking changes in the character of vegetation may be brought about by this factor. For example, grazing of hill pasture by sheep may result in the vegetation being dominated by bilberry (*Vaccinium Myrtillus*) and the grass, sheep's fescue (*Festuca ovina*), where, in absence of sheep, the dominant species would be ling (*Calluna vulgaris*). A parallel case is that of rabbit grazing, which also results in the degeneration of *Calluna* on heath land, and its replacement, as dominant, by grasses (Farrow, 1925). The rabbit-grazing factor is indirectly due to man in Great Britain, as it was he who apparently introduced the animal into this country some time between the beginning of the eleventh and the end of the twelfth centuries (Barrett-Hamilton, 1912). Modification of vegetation by intermittent partial destruction by fire is another indirect biotic effect due to man's activities. This, according to the intensity and frequency of its operation, causes changes varying in degree from a temporary replacement of one dominant species by another, to a complete and more or less permanent alteration of the whole character of the vegetation affected. As an example of the former may be taken the well-known case of the effects of heath fires. On heath land among the subordinate species which are associated with the dominant *Calluna* is usually to be found *Vaccinium Myrtillus*. *Vaccinium* is a plant which, under conditions which are favourable for the vigorous growth of *Calluna*, is unable to compete successfully with it for dominance. It is able, however, to tolerate a considerable amount of shade and so grows amongst the *Calluna* as a shade plant producing rather large delicate pale-green leaves. When a heath fire occurs, the *Calluna*, because of its shallow root system, is usually completely killed, whereas the *Vaccinium*, with its rhizomes running at a depth of some 8 or 9 inches below the surface of the soil, is only temporarily affected (see Fig. 4). The result is, that in the year following the burning, this latter species grows up with renewed vigour and assumes dominance, producing the more robust smaller-leaved 'sun' type of foliage. Meanwhile *Calluna* regenerates from seed, but it is some years before it attains sufficient height and density to regain its dominant position and force back the *Vaccinium* into comparative obscurity. A similar thing happens with regard to bracken (*Pteridium aquilinum*). This species is commonly to be found on heath land in small patches or sparsely growing amongst the *Calluna*. Frequently repeated burning of the *Calluna* often results in a more vigorous and denser growth of *Pteridium* which, for the same reason as is the case with *Vaccinium* (see Fig. 4), is immune from destruction by fire. However, owing to its habit of growth whereby only single fronds are sent up at intervals from its rhizome, *Pteridium* takes longer than *Vaccinium* to produce a sufficiently dense mass of foliage to render it dominant. Repeated burning, however, eventually establishes it in a dominant position, but here the case is rather different from that in which *Vaccinium* is dominant. Dense *Pteridium* casts a greater amount of shade than *Calluna* can tolerate; further, the fronds of the fern can grow to a greater height than that attainable by *Calluna*, so that once the bracken gains complete dominance it retains this position and becomes more or less permanently established.

On areas where the subsoil is loose sand or gravel, these burning and grazing factors may have still more serious results. The outcome of the continued inter-

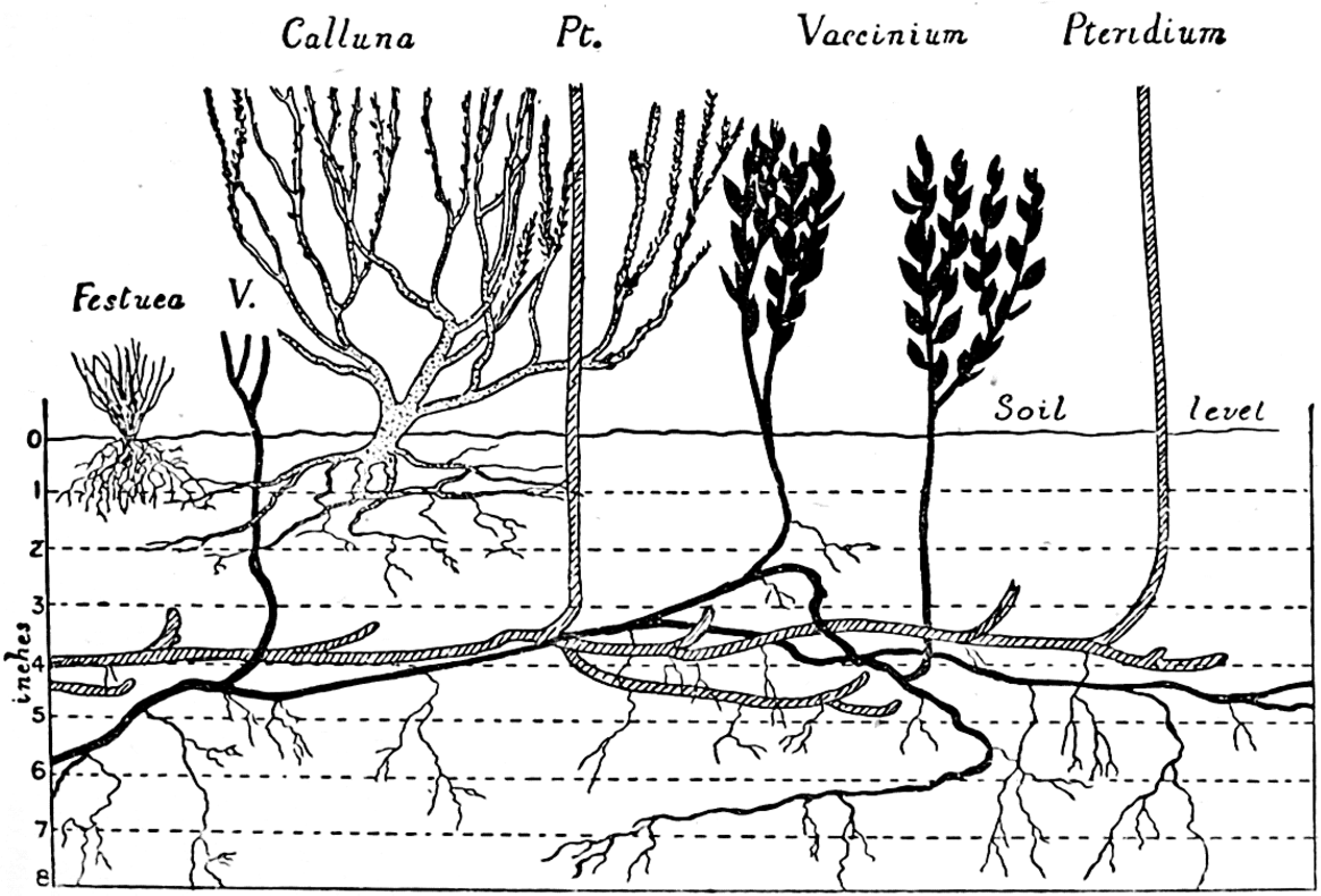

FIG. 4.—Diagram showing the positions in the soil of the root and rhizome systems of heath plants
For further explanation see text

ference may be the total destruction of the surface soil and its reduction to the original state of practically pure sand. Such a substratum is not easily recolonized by vegetation, and trampling by human beings and animals may often prevent more than occasional colonies of mosses like *Polytrichum piliferum* becoming established. The sand surface is loose and unstable, and is readily eroded by wind and rain action so that a bare desert-like area results.

Animals, including man, react on vegetation in countless other ways besides those described in the few more striking cases above. It would be useless to attempt to consider all of them and their nature and reactions. The student in his practical study of the subject will repeatedly encounter them and will, as he gains experience, learn to recognize them.

We will now briefly deal with the interactions occurring between the various plants which grow together to form a plant community. These interactions differ somewhat from the factors we have just been considering, in that they do not always tend to affect the community as a whole in any marked way, but frequently operate more particularly on individual species. Of paramount importance amongst these are the effects due to dominance. The dominant species of a plant community is frequently the largest in point of size, but is always the one which makes the greatest demands on the resources of the habitat. Because of this the dominant species is in many ways the most important feature of a community as it tends to indicate what are the chief habitat factors operating. Under natural conditions, that is, where human interference has for a long period been absent or negligible in degree, the life form of the dominant is chiefly the outcome of climatic conditions, physiographic factors being of subsidiary importance, and biotic factors often still more subsidiary. The actual species acting as dominants depend to a large extent on geographical considerations in regard to what species are locally available. On the other hand, the abundance and floristic composition of the subordinate component of a plant community are to a very considerable degree determined by the nature of the dominant or dominants. This is because they depend in the main on the degree of shade cast by the dominant, the amount of shelter from wind, the resulting atmospheric humidity, the soil water supply, and the nature of the soil as determined by the type of humus produced by the decay of the dead leaves, etc., cast off by the dominant. Similar but less important effects arise from the relationships between one subordinate species and another.

With regard to conditions in the soil, competition for water and mineral salts varies according to the positions of the root systems of the various species. Each species has its roots at a characteristic depth beneath the surface of the soil. Root systems situated in the same layer of soil may be in acute competition with one another for water from the soil, whereas competition between root systems in different soil horizons may be less intense or only slight. Again, roots situated in the surface layer of soil depend largely on direct precipitation for their water, whereas in the deeper layers the water supply may be entirely from upward-moving water from below. This difference in the immediate source of the water supply may obviously be accompanied by differences in the nature and amount of dissolved substances present in the water, and this may have important effects on the species whose roots occupy these respective positions.

From the foregoing brief consideration of biotic influences it will be evident that in many cases they cannot be looked upon as definite factors in the same sense as many climatic and physiographic factors. They are rather biotic modifications or limitations of the latter or their effects. In other cases such as burning and grazing we have definite biotic factors which act directly on the plants themselves, and the effects produced by these are essentially the same as the effects produced by climatic factors under certain circumstances. Burning and grazing, like most climatic factors, tend to operate directly on the aerial parts of the plants. The chief results of their operation is the limitation or prevention of the development of aerial organs ; thus we find two very different factors producing very similar plant communities. For example, periodic burning on a lowland heath may result in a dominance of *Vaccinium Myrtillus* instead of *Calluna* just as climatic factors do on a mountain-top. Similar cases of substitution of one factor for another to produce a given effect on the vegetation are repeatedly to be met with in the field.

PLANT SUCCESSION

A plant community may be compared with an individual organism, in that it is recognized as having a developmental history ; this developmental history is called plant succession. A plant community starts its life in the first place with the colonization of a bare area usually by seedling or sporeling plants. The bare area may be of a dry nature such as a rock or soil surface exposed by weathering, or by a landslide, or by some other physiographic or biotic agency ; on the other hand, it may be shallow water such as a small pool, a silting-up river estuary, or the margin of a lake. On an area of this kind plants eventually appear and become established ; to begin with, this pioneer population is sparse, with more or less wide unoccupied spaces between the individuals which thus form what is termed an *open* community. Later, as is to be expected, the spaces between the plants of the open community become occupied by new arrivals from outside the area, by seedlings from the original colonizers, and by vegetative increase in size of the latter. Eventually all the available soil surface becomes occupied by plants and there is formed what is termed a *closed* community. It will be realized from what has been said that, following on the development of the plant covering to form a closed community, the habitat factors, especially climatic (atmospheric humidity and wind), and edaphic, undergo a change; further, biotic influences come into operation in the manner already described, and produce habitat conditions suitable for plants which make greater demands on their environment than was the case with the original colonizers. This change in habitat conditions, due, as we say, to the *reaction* of the plants forming the community, leads to a change in the plant community itself. Other species gain entry which are more suited than the original colonizers to the changed habitat conditions; they successfully supplant them or by competition greatly reduce their numbers. One or more of the successful new-comers have a higher life form than the original dominants so that one of the most obvious changes that is observed is a change in the dominant species. This change in floristic composition continues and is accompanied by corresponding further changes in habitat factors. The vegetation continues to develop, passing through a series of stages which can often be recognized by changes in the dominant species, each stage usually being characterized by having a dominant of higher life form than that of the preceding stage. Finally, owing to limitations imposed by the local climatic and edaphic factors, a state of equilibrium is reached and the plant community assumes a more or less permanent character. This final and stable type of plant community, the nature of which depends usually on climate, though in certain circumstances soil may affect it, is termed the *climax* type. Frequently some one biotic or physiographic factor is sufficiently intense and permanent in its operation to arrest the development of a plant community, and to maintain it at some stage before the true climax is reached. Such a community is termed a *sub-climax* type. Plant succession is the term used to denote this developmental process of plant communities in a general and abstract way. If one is referring to a definite concrete example of plant succession, such an example is termed a *sere* and the various stages of the sere are called *seral* stages or *seral* communities. Furthermore, it is customary to distinguish between seres that originate on areas which never within recent geological times have supported vegetation, and those on areas which have at one time had a covering of plants, but from which the plants have been, by some agency, subsequently removed. In the case of the former the sere is *primary*, while in the case of the latter it is *secondary*. The chief point regarding this distinction is, that in the case of a primary sere the initial bare area entirely lacks any of the habitat modifications brought about by plant reaction, the main feature implied being that the substratum is entirely inorganic in construction. The area on which a secondary sere develops has retained some of the effects resulting from the reactions of the original plant covering; what these residual effects amount to depends on the nature and intensity of the destructive agent which removed the vegetation. It will be realized here that soil development runs parallel with plant succession and must always be considered along with it.

It has been pointed out above that a bare area which initiates plant succession may be wet or it may be dry. In the first case the pioneer stages in the succession will consist of species of a hydrophytic nature. As succession proceeds, the plant reaction tends to render the habitat drier by adding organic matter to the soil and raising its level above that of the water. On the other hand, when the bare area is dry, the pioneers may be more or less xerophytic, the degree of xerophytism depending on local climatic and physiographic factors. In this case there is a tendency for the developing vegetation, by adding organic matter to the soil, to increase the water-holding capacity of the latter and so to render the habitat more moist. This change in habitat conditions is further augmented by the increase in atmospheric humidity brought about by the presence of the colonizing plants. A sere beginning on a wet area is often referred to as a *hydrosere* and one beginning on a dry area as a *xerosere*.

It will be readily understood that in temperate regions like Great Britain, both of these types of sere converge during their development to produce mesophytic habitat conditions, that is, conditions which are neither excessively dry nor excessively wet. It must be remembered, however, that a mesophytic climax can only develop if the climate is of a suitable type. For example, in a region where the climate results in desert or semi-desert conditions, a xerosere would begin and end with xerophytic vegetation.

Plant succession is of universal occurrence wherever vegetation exists ; this is because destructive agencies which result in a partial or total local removal of the vegetation are found to be frequently in operation. The student in the field therefore experiences no difficulty in finding examples for study, of seres in all stages of development. In fact, in a country like ours where most of the vegetation is always more or less affected by the direct or indirect modifying influences of man, the majority of the plant communities encountered show some stages of successional development.

To quote a few examples there is first the already mentioned result of the burning of *Calluna* on heath land. The fire destroys the vegetation including the dominant *Calluna* and usually some part of the upper soil horizon. The removal of the *Calluna* reduces the cover and renders the habitat drier by allowing increased direct evaporation from the soil ; increase in the abundance of aerial shoots of the surviving *Vaccinium Myrtillus* takes place so that this species becomes the dominant of a seral community which develops on the site of the original *Calluna* heath. Gradually *Calluna* seedlings reappear and become established along with other of the original heath plants which suffered destruction. The *Calluna* grows up and overshadows the *Vaccinium* once more as it regains dominance. The shade increases and the surface horizon of the soil, which was more or less destroyed by the burning and subsequent drying, becomes re-formed by the accumulation of dead plant remains. The habitat conditions become generally more moist so that such xerophytic bryophytes as *Polytrichum piliferum* and *P. juniperinum*, which are usually in evidence in the early stages of such xeroseres, are slowly replaced by the original shade and moisture-loving types like *Hypnum cupressiforme* and various leafy liverworts. Thus a partial destruction of a heath community by fire initiates a xerosere, whereby a number of seral stages ensue and lead finally to a regeneration of the original type of heath community. This burning is usually deliberately carried out periodically by gamekeepers on grouse moors for the purpose of providing young and tender shoots for the birds to feed on. This persistent recurrence of the initiating agent of the succession may in places result in the *Calluna*-dominated stage never being attained, when a sub-climax community dominated by *Vaccinium Myrtillus* may be the highest type reached. Somewhat similar sub-climax heath communities may result from grazing by sheep or rabbits, the persistence of which may bring about the suppression or extermination of the otherwise dominant *Calluna* on heath land, giving a grass, or grass and *Vaccinium*-dominated sub-climax. This effect of rabbit grazing has been investigated and described by Farrow (1925) on the East Anglian heaths, and one of a similar nature produced by sheep on hill pastures has already been mentioned (see p. 44). It may be pointed out here that much of the *Calluna* heath in this country must be considered to be of the nature of a sub-climax, due to the continued operation of biotic factors arising out of the direct or indirect interference of man, which has prevented the successional development of a climax forest community.

In most places the dominant tree of this climax forest was originally oak, but on certain sandy soil areas Scots pine now appears to be the tree most suited to the habitat. This change from oak to pine as the climax dominant, can probably be explained in terms of soil alterations which set in when the oak forest was destroyed. The removal of the trees would lead to rapid deterioration of the original brown-earth soil, and with the development of heath vegetation, soil processes came into operation which finally resulted in the replacement of the brown-earth soil by podsol. This, on account of its acidity and deficiency in bases, would not favour the regeneration of deciduous forest. On the other hand, it would support pine forest which, under the circumstances, should now probably be considered to be the natural climax for such areas.

In the example described on page 52, of plant succession initiated by the burning of heath, the sere is comparatively short as the whole of the original vegetation is not removed by the fire, and the soil may only be changed to a slight extent. Frequently one encounters cases in which secondary succession is initiated by far more drastic modifications of the habitat. The vegetation may be wholly destroyed and the soil so altered as to render the resulting succession almost primary in nature. Such cases are, for instance, to be found on sandy areas where various human activities have resulted in a bare soil surface of almost pure sand from which organic material is practically absent. The sere on such a sand surface is almost primary in type and usually begins with bryophytes as the first colonizers. Spores of *Polytrichum piliferum* or *P. juniperinum* germinate and produce an open community of moss shoots which connect with a dense rhizoid system which permeates and binds together the top few millimetres of sand. The *Polytrichum* shoots increase in number until a close carpet of moss is formed over the soil in which seedlings of higher plants such as *Festuca ovina, Calluna vulgaris, Galium saxatile*, etc., are able to germinate and become established. The reaction of the pioneer moss is thus, to begin with, the stabilization of the soil surface and the increase in its water-retaining capacity. As the moss shoots become more numerous and form a closed community, the dead parts of the plants add to the amount of organic matter in the soil and still further increase its water-holding capacity. In this way the habitat is rendered suitable for the germination of the seeds of higher plants and these, as they grow in size, continue the soil-modifying reaction and make the habitat more and more suitable for the support of still larger plants. Increase in the shade cast by the higher plants results in a gradual suppression of the *Polytrichum*, and the immigration of shade-loving mosses into the community. Active competition between the phanerogams, which tend to become crowded, takes place and as the *Calluna* becomes definitely established as dominant, the total number of plants of all species tends to decrease. This latter state of affairs is to be expected as the various plants grow to maturity and individually increase in size. During this active competition stage the relative frequencies of the different species present undergo changes until a balance is reached between them in respect of their individual requirements. Competition then becomes less intense as the community becomes stable and a climax state is reached. Regarding the soil processes taking place, it will be clear that in this case as in the last, they will tend towards the development of a podsol profile.

From a consideration of the foregoing examples we see that succession, whether primary or secondary, hydrosere or xerosere, is more or less characterized by a similar series of stages which may be enumerated as (1) *nudation*, or the formation of the bare area, (2) *colonization*, (3) *ecesis*, a term used to denote the establishment and attainment of maturity of the colonizing species, (4) *reaction*, (5) *competition*, (6) *stabilization*, and (7) *climax*. The subdivision of seres into primary and secondary is chiefly of importance in relation to soil development, which may have a far-reaching influence on the type of vegetation that ultimately becomes established. In a general way this latter is bound up with whether the soil processes give rise to acid conditions with a low base content or to neutral conditions and a higher base content.

As a definite example of primary succession, we may consider the one which begins with the development of a salt marsh along the shore of a river estuary. First of all silt forms an accumulation which is exposed at low tide and submerged at high tide, thus providing a suitable station for colonization by salt wort (*Salicornia europaea*) which forms an open community on the mud. The reaction of the *Salicornia* is to reduce the rate of movement of the water during the submerged phase at high tide so that more silt collects and raises the level of the mud with the result that the period of submergence is reduced. The grass *Glyceria maritima* then gains entry and by its numerous shoots still further increases the accumulation of silt which it stabilizes by means of its abundant fibrous roots. As the silt deposit continues to increase the habitat becomes drier so that *Festuca rubra* enters, successfully competes with the *Glyceria* and becomes temporarily dominant, meanwhile continuing the soil-accumulating reaction. The soil level thus becomes completely raised above the level of the water except during high spring tides. The habitat is now definitely drier, and the downward percolation of rain-water reduces the amount of salt in the soil. The soil level continues to rise and soil organic matter continues to increase. Further seral stages, marked first by the dominance of *Armeria maritima* and later of *Juncus maritimus*, are passed through, leading to heath land or other sub-climax vegetation or possibly to a forest climax.

It would be possible to continue indefinitely to describe examples of plant succession and to elaborate such descriptions by a consideration of the subordinate species which accompany the dominants of the various seral stages. The few cases dealt with above should suffice to give the beginner a clear idea of the more important features of the phenomenon and to serve as an indication of what to look for during practical study in the field.

CLASSIFICATION OF PLANT COMMUNITIES

We have seen that plant communities possess individuality and that they can be compared with living organisms in that they may pass through a number of developmental stages and finally attain a relatively stable maturity which we call a climax or sub-climax as the case may be. If the vegetation of an area of considerable extent be examined, it will be found that the plant communities present are of a number of types, the nature of each being determined by the local habitat conditions under which it exists. As there may recur in different parts of the area similar combinations of habitat factors, so we find a corresponding recurrence of a given type of plant community. For example, during a day's walk in the country we may encounter a number of times in different places such plant communities as *Calluna* heath, oak wood and reed swamp. Further, all the plant communities encountered are not of the same degree of importance, as some types will be found to recur much more frequently and to cover a much greater proportion of the area than others. In order to render simpler and more precise the description of plant communities and to facilitate their comparison one with another, ecologists have found it expedient to classify them. The classification of plant communities has presented considerable difficulties, and has evoked a good deal of controversy at various times, chiefly between workers living in different parts of the world. This has been largely on account of variations in the relative importance of certain ecological factors, in the determination of the main features of the vegetation in these different regions (Tansley, 1920).

The largest vegetation class now generally recognized by British ecologists, apart from the great climatic divisions, is the plant *association*. It is uniform in type so far as the general characters and life form of the dominant species are concerned, it exists under broadly uniform habitat conditions and is within reasonable limits definite in its floristic composition. Associations are usually designated according to the nature of their dominant species; we thus have the deciduous forest, the coniferous forest and the heath associations occurring in Great Britain. It is obvious that the name plant association refers to plant communities which have definitely reached a stable climax state and that it cannot logically be applicable to types of vegetation which are seral stages and which will eventually give place to the local climax type. Thus we cannot legitimately class reed swamp as an association although we frequently find it referred to as such, because we know that this type of community is only a stage in the hydrosere which begins with shallow water and usually ends with forest or other climax vegetation.

A plant association has commonly more than one dominant species, because it is usually composed of a number of smaller unit communities each of which has its own dominant. For instance, within the deciduous forest association in Britain we find communities dominated by the oak, the ash and the beech ; this is chiefly the outcome of local differences in soil factors. These smaller communities, each having a single dominant apart from minor variations, are termed *consociations*. Minor communities within the consociation, owing origin to localized factor variations, or to other causes, and dominated by other species, not the association or consociation dominants, are known as *societies*.

A corresponding system of classification is sometimes used in connexion with seral communities. Thus we have the already-mentioned reed swamp community which corresponds in general features with an association, but as it is only a developmental stage, cannot be designated as such. The reed swamp is therefore called an *associes*. Similarly, seral communities which correspond in rank with the consociation and the society are respectively given the names *consocies* and *socies*. On this basis, the birch wood which usually springs up naturally on the site of an oak wood after the oaks have been felled, is a *consocies*, as also is the transient *Vaccinium Myrtillus*-dominated community that characterizes the sere following a heath fire.

When describing a plant community it is usual to employ the term *status* to denote its successional stage and its relationships with other plant communities. Thus the seral birch wood mentioned above has a different status from the climax birch forest that occurs in the north of Norway or on the mountains in Scotland.

CHAPTER III

THE PRACTICAL STUDY OF PLANT ECOLOGY

HAVING dealt in the last chapter with the general principles of plant ecology, it is now necessary to consider the methods whereby the practical study of these principles can be carried out. As the greater part of such practical work must be done in the field, and as for various reasons it may not always be possible to visit at will the area in which the field investigations are being made, it is essential to make observations and to conduct experiments in a systematic manner. The results of these experiments and observations should always be recorded in the form of careful notes made while actually on the scene of operations, as, if one postpones the writing up of records of field work until some later time, there is a possibility that important details may be omitted or inaccurately described.

In general, when taking up the study of the vegetation of an area, the work falls into two divisions, namely, (*a*) preliminary reconnaissance work, and (*b*) more specialized detailed studies of particular aspects of the subject.

RECONNAISSANCE

Reconnaissance involves the recording of the chief features of the plant communities present and the more obvious effects of ecological factors on these communities, over a region of considerable extent. It is usual to carry out reconnaissance when beginning a study of the vegetation of a new area, as it forms a preliminary to a more detailed study of those sections of the area which present features of special interest. Reconnaissance studies, when done in considerable detail and supplemented with photographs and vegetation maps showing the characters and distribution of the plant communities present, are usually referred to as *primary surveys*. Primary surveys, in addition to serving the already-mentioned preliminary purpose, may in themselves be of considerable value as records, particularly in regions where, owing to the intensive operation of biotic influences such as man's activities, or of other ecological factors, the vegetation is liable to undergo comparatively rapid modification.

When conducting a reconnaissance the first thing to do is to travel about in the area which is being studied and to note the more important plant communities and their distribution in relation to the main habitat factors. If time allows, these plant communities and their distribution should be indicated on a map; six-inch Ordnance survey maps are useful for this purpose. While in the field the characteristic features of these communities should be recorded together with lists of their component species. In these lists, the frequencies of the various species should be indicated by means of symbols in the manner described below.

When mapping vegetation it is advisable for the sake of uniformity to employ the recognized symbols to denote the different types of vegetation as used by British ecologists, some of which are shown in Fig. 5 (see *Journal of Ecology*, **8**, p. 66, 1920). In this figure it will be noted that basis symbols are used for general types of plant communities such as woodland, moorland, heath, etc., and that these can be particularized by adding further symbols for the purpose of denoting the dominant species. Where mapping is carried out on six-inch Ordnance survey maps, the symbols for the dominants should be included, but if smaller scale, such as one-inch, maps are used, only such general features of the vegetation as can be shown by means of the basis symbols should be indicated.

With regard to the making of lists of the species which make up the floristic compositions of plant

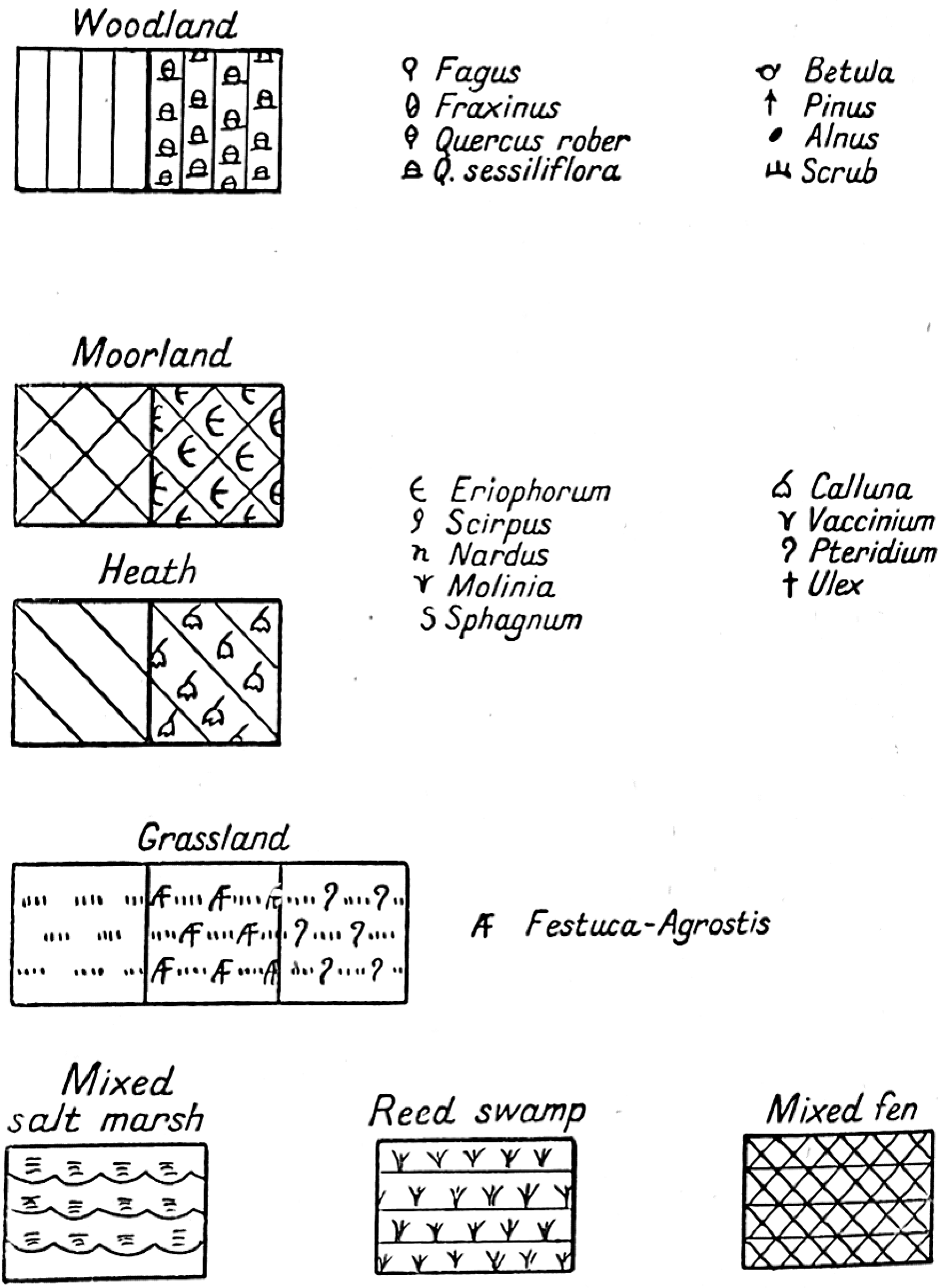

FIG. 5.—Symbols used in mapping vegetation. In the cases of woodland, moorland, heath and grassland, basis symbols are shown on the left of the diagrams. Special symbols for dominants are shown on the right and their method of use is indicated in the diagrams

communities it is usual to append a letter after the name of each species to denote the frequency of its occurrence in the community. The letters in general use for this purpose and their meanings are given below:

d	dominant,	f	frequent,
va	very abundant,	lf	locally frequent,
a	abundant,	o	occasional,
la	locally abundant,	r	rare.

Variability in the frequency of a species between two of these values is usually shown as—o to f, or f to a (occasional to frequent, or frequent to abundant).

It is difficult to describe clearly exactly what value one should attach to these symbols, and it may appear that considerable discrepancy will occur between the frequencies as estimated by different workers. In practice, however, it will be found that after a certain amount of experience has been gained by making lists in the field and deciding upon the frequencies of the species listed, a standard will usually be arrived at which will not differ greatly from that in general use amongst experienced ecologists. As an example of such a list, the following may be taken; it gives the floristic composition of a regenerated heath community six years after the original heath was burnt, and which has developed on a dry south-facing slope in the Lake District.

Calluna vulgaris	va, d.
Erica cinerea	o to f.
Pteridium aquilinum	o to f.
Vaccinium Myrtillus	f.
Thymus serpyllum	o.
Galium saxatile	o to lf.
Potentilla erecta	o.
Campanula rotundifolia	o to lf.
Polygala serpyllacea	o to lf.
Festuca ovina	a.
Agrostis tenuis	o to f.
Deschampsia flexuosa	f to a.
Holcus lanatus	f.
Nardus stricta	o.

With regard to the type of notebook most suitable for use in the field, different workers may have different preferences. After considerable experience of various types the writer has found ordinary duplicate books $8\frac{1}{2}$ in. by $5\frac{1}{2}$ in. in size, with numbered pages, to be the most generally useful. The fact that a carbon copy of all notes is obtained, which can be removed at the end of the day, is an advantage in that the danger of accidentally losing the records of one's work is minimized. Further, a single notebook can be used for work on different areas, the copies being sorted out and correctly grouped afterwards. It is also convenient to have a pencil attached to the book by a piece of string in order to save oneself the possible annoyance of its temporary or complete loss.

It is not proposed to go into further details regarding the methods used in reconnaissance and primary survey as this work should, as a rule, only occupy a fraction of the time spent in ecological study. The chief purpose of it is to familiarize oneself with the plant communities with which one is likely to deal and to give some idea of what problems are available for detailed investigation.

DETAILED STUDIES

Detailed studies, of the relationships between particular plant communities and habitat factors, of successional changes taking place in plant communities and of the causes which bring about these changes, should form by far the most important part of practical field work in plant ecology. With regard to the first of these aspects, the work should chiefly consist of the careful investigation of habitat factors and their operation within a circumscribed area. The way in which variations in these factors bring about variations in the plant communities present should also be studied. By accumulating data concerning these variations in habitat factors which accompany parallel variations in vegetation, we shall help towards the solution of problems regarding the actual way in which habitat factors affect the individual plants. As plant succession is largely bound up with gradual change in habitat factors, this aspect must also be continually borne in mind even when it does not form the immediate subject of study.

In the carrying out of an investigation of this kind the work falls into four sections, namely :

I. A careful examination of the floristic composition and the status of each of the plant communities involved.

II. As complete an investigation as possible of the habitat factors of each plant community.

III. An examination of the successional features presented by the plant communities.

IV. Correlation of the results of the above investigations.

Regarding Section I, the work is comparatively straightforward and the method used in the listing of species and the indicating of their frequencies has already been dealt with (cf. p. 61). Where gradual transition occurs between one plant community and another, careful lists should be made to indicate the changes occurring in the species and their frequencies as one passes across the intermediate zone between the two communities. Similarly, slight local changes in the composition of a plant community, which result from some local change in habitat factors, should be carefully noted. Care should be also taken accurately to identify all species recorded and where doubt exists as to accuracy of identification, pressed specimens should be kept for purposes of verification.

In the case of Section II, investigations for the most part of an experimental character have to be carried out in order to determine as far as possible the nature and intensity of each individual habitat factor in operation. Owing to the already-mentioned inadequacy of field methods this investigation of habitat-factor problems cannot be conducted in as complete a way as one might wish. A considerable amount of useful work, however, is possible with the methods at our disposal and until others are devised we must do the best we can with them.

Investigation of Habitat Factors

Climatic Factors.—The general climatic features of a region can usually be obtained from local meteorological records. Such general climatic data may be important if the field of study covers an extensive area. They are important in relation to considerations as to what is the climax type of vegetation characteristic of a region and are also useful where the vegetation of one region is to be compared with that of other regions which have different climates. In the case of the student of ecology residing in Great Britain, practically all of his studies will be carried out in areas of relatively small extent in which general climatic conditions are practically uniform apart, of course, from local modifications caused by topographic features. The study of climatic factors may therefore be practically confined to that of local variations in relation to topography.

Physiographic Factors : (*a*) *Topographic Factors.*—For the study of these the student requires to note variations in altitude occurring in the area under consideration ; these may be determined approximately from a contour map, or they may be measured by means of an aneroid barometer if one is available. Altitude is important in that it may be responsible for certain local climatic factors. The exposure of slopes should be determined by taking compass bearings, and the angles of slopes should be measured by means of a clinometer. Information so obtained is necessary when considering insolation (see p. 18) which, in turn, may indirectly affect local temperature and atmospheric humidity. Slope, as we have seen, is also important in connexion with its influence on soil stability and on the movement of soil water and its effect on soil erosion, aeration, etc. Although clinometers may be purchased as separate instruments or combined with a compass, a satisfactory one may be improvised from an ordinary protractor and a thread having a weight attached to its end to form a plumb line. When considering the effect of slope it is necessary to ascertain the direction of the prevailing winds, and to look out for indications of wind action on the vegetation ; this, in exposed places, may be an important factor in determining the dominant species.

Atmospheric humidity determinations can be carried out with an ordinary wet-and-dry bulb thermometer, but as this is somewhat slow in reaching a steady reading it is better to substitute it by the type which has a handle hinged at the end away from the thermometer bulbs, by means of which it can be whirled round. Such an instrument is termed a *sling hygrometer*.

(*b*) *Edaphic Factors*.—Owing to the extreme importance of the soil factors as determiners of the characters of plant communities they should be investigated as completely as possible. For the rapid examination of soil characters a necessary piece of apparatus is some form of soil borer by means of which soil samples can be easily obtained from various depths below the surface. The most satisfactory type is the soil auger as used by soil surveyors in this country. It consists of a one-inch diameter and one-inch pitch wood auger welded or otherwise attached to a tubular shaft so that the whole instrument is about three feet six inches long, and fitted with a cross-bar at the top to serve as a handle to enable it to be screwed into the soil. In use it is screwed into the soil to a depth of about nine inches and then pulled up, the soil is retained by the twist of the auger and can be removed for examination; the auger is then reintroduced into the same hole and another nine inches sampled. This process is repeated until the whole soil profile has been examined down to the parent soil-forming material. In this way the various soil horizons can be rapidly examined and the soil type and its characteristic features noted. When using the soil auger one should note the degree of wetness exhibited by the different horizons and also note their texture and colour. With regard to texture, with a little practice this can be determined by the feel of the soil when it is rubbed between the thumb and finger. A number of symbols are used in this country to indicate soil texture; they are as follows:

Light sand	Sa.	Light silt	Za.
Loamy sand	Sb.	Medium silt	Zm.
Light loam	La.	Heavy silt	Zb.
Medium loam	Lm.	Peat	P.
Heavy loam	Lb.	Clay-sand	cS.
Clay	C.	Sandy clay	sC.

The texture of the soil gives a rough indication of its mechanical composition, a feature which is important in relation to water content, water movement and soil aeration.

Special notice should be taken of any sign of red-and-yellow mottling in the lower horizons as this is a certain indication of impeded drainage, a feature which is practically always reflected in the vegetation growing at the surface.

The soil profiles beneath plant communities which are being specially studied should be carefully examined, preferably by digging a hole and exposing a section. Samples of soil from the different horizons should be collected and taken away for the purpose of carrying out mechanical analyses and estimating organic matter and water content.

The soil samples should be collected in tins with tightly fitting lids and weighed in the fresh state immediately on returning to the laboratory. The contents of the tins may then be spread on sheets of paper in the laboratory and left for a few days until air dry, or preferably they should be dried on a hot plate at about 40° C. The samples should then be weighed again, the differences between the initial and final weights giving the amount of loosely-held water they contained. The samples should then be pounded up with a wooden pestle, passed through a 2-mm. sieve to remove the stones, which should be weighed. The fine soil should then be dried to constant weight in an oven at 105° C. The difference between the sum of these two last weights and the first weight of the fresh soil will give the total water content.

Water-content estimations of soils, as indicated by the differences between fresh and air-dry weights, in themselves are often of considerable value when investigating the reasons for local changes from one type of plant community to another. If all the samples are collected together and dried under identical conditions the results obtained are reasonably comparable. For example, such a set of samples examined in the Lake District, where a community dominated by *Nardus stricta* adjoined a community dominated by *Eriophorum angustifolium*, gave a soil-water content of 38 per cent. under *Nardus* and 81 per cent. under *Eriophorum*. In each case the soil was collected from round the roots of the dominant plants. Where possible, however, such estimations should be carried out at intervals throughout the year in order to give more complete information as to seasonal variations of soil-water content.

Mechanical Analysis of the Soil.—The dry soil sample, which has been passed through a 2-mm. sieve as described above, is dealt with as follows :

1. Weigh out 10 gm. of the sieved soil, place in a beaker, add 60 c.c. of 6 per cent. hydrogen peroxide and heat to 100° C. over a water bath with repeated

stirring until effervescence ceases. Add further hydrogen peroxide in 50-c.c. portions, repeating the process until no further action takes place. This oxidizes and renders soluble the humified organic matter.

In some soils the presence of manganese dioxide hinders the process by rapidly decomposing the hydrogen peroxide. When this occurs the soil should be digested in 20 c.c. of 1 per cent. to 2·5 per cent. sodium hydrogen sulphite solution until almost dry, before treating with hydrogen peroxide as described above.

2. After cooling, add sufficient water and hydrochloric acid to give about 100 c.c. of soil suspension in approximately 0·2 N hydrochloric acid. Excess of acid will be required if the soil contains more than about 5 per cent. of carbonates. Allow to stand for one hour with frequent shakings.

3. Filter, pouring the filtrate back if it is turbid, and wash the residue three times, using each time 50 c.c. of distilled water. Spread the filter paper on a large watch-glass and wash the soil with a jet of hot water on to a 70-mesh (0·2 mm.) sieve. With a rubber pestle and under a jet of water rub as much of the soil through the sieve as will pass. Dry at 105° C. and weigh the residue which is left on the sieve. This is the coarse sand fraction.

4. Make up the suspension of fine particles which has passed through the 70-mesh sieve to from 300 to 400 c.c., add to it 4 c.c. of N-sodium hydroxide solution and pour into a pint bottle. The bottle should then be shaken for two hours on a reciprocating shaker or for six hours on an end-over-end shaker.

5. Transfer the suspension to a measuring cylinder, make up to 500 c.c. and adjust its temperature to 20° C. Shake for one minute by repeatedly inverting the cylinder and allow the suspension to stand for four minutes forty-eight seconds. At the end of this time carefully withdraw, by means of a pipette

with its point exactly 10 cm. below the surface of the liquid, a 20-c.c. sample. This sample contains silt and clay (particles less than 0·02 mm.); it should be run into a previously weighed porcelain dish dried at 105° C. and weighed. The weight of this silt and clay in milligrams divided by four will give the combined percentage of these fractions present in the soil sample.

6. Again shake the suspension for one minute and allow it to stand for eight hours, then again remove 20 c.c. at a depth of 10 cm. This contains the clay fraction only, and by treating it exactly as described above for the clay and silt mixture, the percentage of clay (particles less than 0·002 mm.) in the sample may be found. The percentage of silt (particles 0·02–0·002 mm.) is then found by subtraction.

7. To determine the fine sand fraction (0·2–0·02 mm.), pour away most of the supernatant liquid after the clay sample has been taken and transfer the sediment to a 400-c.c. beaker. Add water at 20° C. to a depth of 10 cm. from the bottom of the beaker. Stir up the suspension thoroughly and allow it to stand for four minutes forty-eight seconds to allow the fine sand fraction to settle, then decant the turbid liquid from the sediment. Repeat this process with fresh water until the supernatant liquid is clear at the end of the settling period. The sediment which is left is the whole of the fine sand that was present in the original soil sample.

Estimation of the Soil Organic Matter.—There is as yet no really satisfactory method known for the estimation of organic matter in soils. However, in the case of sandy humus soils containing a negligible amount of calcium carbonate the loss on ignition gives a rough measure of the amount of organic matter present. If clay and silt are present, the loss of combined water from these introduces serious error.

If a considerable amount of calcium carbonate is present, this can be estimated by treating a weighed quantity of dry soil with dilute acid and measuring the amount of carbon dioxide evolved. A convenient apparatus for carrying this out is the Collins calcimeter (see *Journal Soc. Chem. Ind.*, 1906, **25**, p. 518).

As the carbon dioxide of carbonates is driven off during ignition, estimations of organic matter by this method may be too high. A correction for this error can be applied from the results of the carbonate estimation described above.

It may be considered necessary, in connexion with certain vegetation problems, to carry out complete soil analyses. If this is the case the student should consult the special works which deal more fully with this subject (see Russell, 1932, and Robinson, 1932).

Determination of Soil Reaction.—Measurements of the hydrogen ion concentration of the soil will chiefly be done in the field by the colorimetric method. The most convenient outfits for this purpose are made by the British Drug Houses Ltd., and are sold under the name of 'Capillator' outfits. For the approximate determination of the *p*H of soil, this firm has prepared a special mixture of dyes which they call the 'B.D.H. Soil Indicator.' This mixture when added to soil takes up colours ranging from red through orange yellow and green to blue according to the *p*H of the particular soil used ; red indicating a *p*H of 4, orange 5, yellow 6, green 7, and blue 8. The Capillator outfit for this indicator consists of a bottle of the soil indicator, a bottle of distilled water, a small watch-glass half an inch in diameter, a supply of capillary pipettes and a card on which is mounted a set of sealed capillary tubes containing solutions of the indicator of definite *p*H values. The capillary tubes are mounted in threes so that they form a series of coloured strips each marked with its exact H*p* value. In use, the watch-glass is about one-quarter filled with the soil to be tested and a definite quantity of distilled water is added to the soil by means of one of the graduated capillary pipettes. A similar quantity of the indicator is also added to the soil which is stirred up and allowed to stand for about one minute. The indicator solution is then again drawn into the capillary pipette and its colour is compared with the card of standards which covers a *p*H range from 4 to 8 in steps of 0·5. In this way the approximate *p*H of the soil sample is determined. For more accurate determinations, Capillator outfits can be obtained for individual indicators of much narrower range. In these the standards provide for differences in *p*H of 0·2. A convenient series of these indicators which covers the range required for most field work is :

Bromo-cresol green . . .	*p*H 3·6–5·2
Bromo-cresol purple . . .	*p*H 5·2–6·8
Bromo-thymol blue . . .	*p*H 6·0–7·6
Phenol red	*p*H 6·8–8·4

For very approximate estimations of soil reaction the 'B.D.H. Soil Testing Outfit' as put up for the use of farmers is useful owing to the simplicity of its manipulation. It consists essentially of a bottle of 'B.D.H. Soil Indicator' and a small porcelain boat in which a quantity of the soil to be tested is treated with a few drops of the indicator. No standards are used, the *p*H is simply estimated, by inspection, from the colour taken up by the indicator.

The Artificial Modification of Edaphic Factors.—The experimental modification of existing edaphic conditions often produces striking corresponding changes in vegetation. Where the actual factor modification is understood, such experiments may be of considerable ecological value. For example, Farrow (1925) found that on grass heath with *Festuca ovina* and *Agrostis tenuis* as co-dominants, artificial increase in the soil water by irrigation caused the *Agrostis* to become completely dominant with the result that *Festuca* was crowded out. In Farrow's experiment the irrigation was carried out by allowing water to drip from a tap fitted to a barrel which was periodically filled up. When carrying out experiments of this kind, the floristic composition and other features of the vegetation of the experimental area and also of an adjacent unmodified control area should be carefully recorded periodically. Soil conditions may be experimentally modified in other ways than the above ; for example, soil water content may be reduced by drainage, or substances such as calcium carbonate or salts containing nitrogen, potash, sulphur, etc., may be added to the experimental area and their effects observed and recorded.

Biotic Factors.—When we come to investigate the operation of biotic factors we find that they can be divided into two groups. The first group includes those factors arising out of the activities of man and grazing animals, and whose origin is, as it were, external to the plant community. The second group contains all those factors which result from the interactions between one plant and another within the community and which we may consider as internal in origin. The first of these groups differs from the second in that the intensities of the factors are capable of being easily altered whereas in the case of the second group direct modification may be impossible or very difficult.

Complete information as to the activities of man and of grazing animals on an area of more or less natural vegetation such as heath or forest is often difficult to obtain. The effects of one of these factors can usually be estimated to a considerable degree of accuracy if it is possible to compare the vegetation of one area with that of an adjacent area on which the particular factor under consideration is known to operate with greater or less intensity. A case in point is the grazing effect described on page 44. Where such facilities for comparison are absent, information regarding the effect of a factor may only be obtained by eliminating it on part of the area that is being studied. Large animals such as cattle and sheep may be excluded from an experimental plot by wire fencing, while for rabbits and smaller animals wire netting of a suitable mesh should be used. This latter should be let into the ground for about six inches and should have its lower edge turned outwards for about six inches to prevent the animals burrowing beneath it.

Information regarding the effects of the various activities of man, such as burning, draining and coppicing, can usually be obtained by making inquiries of local landowners, gamekeepers, etc., as to the extent to which such operations have been carried out. Useful facts regarding the past history of the vegetation of an area can sometimes be learned from historical records, although this avenue of inquiry is often disappointingly unfruitful.

The study of what we have termed the internal biotic factors operating in a plant community involves a diversity of questions. In the first place the shade cast by the dominant species affects the rest of the community, and the light intensity within and outside the community is therefore an important factor. Then there are such questions as atmospheric humidity within the community, competition between both aerial parts and underground structures of different members of the community, and the effect of the community on soil structure and development.

An estimation of the degree of shade prevailing within a plant community can be carried out in a fairly satisfactory way with the aid of an ordinary photographic actinometer. In this instrument a piece of sensitized paper is exposed to the light and the length of time taken for it to darken to the same colour as a standard tint is noted. In carrying out a light-intensity determination within a plant community the actinometer should be continually moved about while the exposure is being made in order that an average reading may be obtained. This measurement is immediately followed by another taken out in the open while sunshine conditions are the same. The result is recorded as the ratio of the light intensity within the community to that out in the open.

Comparisons between the atmospheric humidity within the shelter of a plant community and outside it should be made. Where woodland is being studied, these can be carried out with the aid of a sling hygrometer as already described on page 67. If, however, the community under consideration is dominated by low shrubs or herbs as, for example, *Calluna* or *Pteridium*, it will be necessary to use some instrument which requires less space for its manipulation, such as an ordinary wet-and-dry bulb thermometer or, if one is available, an aspiration psychrometer. In the latter instrument the wet-and-dry bulb thermometers project into a tube which is open at one end and at the other is connected to a clockwork fan. The fan draws air through the tube at a uniform rate past the thermometer bulbs, and in use the apparatus is held with the air intake aperture in the locality where it is desired to make the humidity estimation.

Measurements of atmospheric humidity are carried out in this way in order to obtain information with regard to the transpiration rates of the plants forming the lower strata of the plant community. As transpiration is largely governed by the same laws as evaporation, temperature and air movements as well as atmospheric humidity should be taken into account in investigations of this kind.

An apparatus which automatically integrates all three of these factors and directly measures evaporation rate is known as an *evaporimeter*. Elaborate evaporimeters are obtainable, but ordinary comparisons of evaporation rates in adjacent plant communities and in their different foliage strata can be carried out with simply constructed instruments of the 'Livingston' type. Such an instrument is shown in Fig. 6 and it will be seen that it consists of a small porous pot, A (pots measuring about 1 in. by 3½ in. are easily obtainable), filled with water and fitted with a rubber bung and connected by a glass tube to a bottle, B. On the neck of the bottle is scratched a mark, C, and at the beginning of an estimation water is run into the bottle until the level stands at this mark. Evaporation takes place at the surface of the porous pot and so water is withdrawn from the bottle. At the end of a predetermined period of time, water is run into the bottle through tube D from a burette until the level again stands at the mark on the neck. The amount of water required for this is measured by means of the burette and is the amount lost by evaporation during the experiment. While in use, tube D should be covered with a loosely fitting specimen tube as shown in the figure.

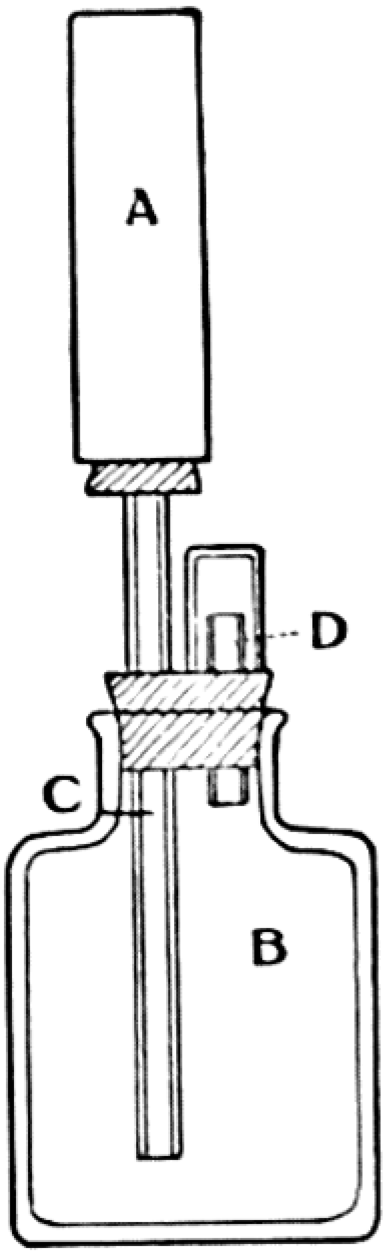

Fig. 6.—Diagram of a simple type of Livingston Evaporimeter

For description see text

If a number of such evaporimeters are set up, they may be standardized with one another by being all started together under identical conditions in the laboratory and allowed to evaporate for a time. At the end of the time the rate of evaporation from each can be measured as described above, and having obtained these rates one may be taken as unity and factors calculated for the purpose of reducing the rates of all the rest to this standard.

Attention should be paid to the underground organs of the various species in a plant community. The structure, mode of branching and positions of these organs in the soil will be found to help in the direction of explaining the presence of their possessors in the community. Possibility of root competition should be considered; the soil horizons occupied by the root systems of different species will be significant. It will be realized that limitations of space may frequently be much more acutely experienced by these underground organs than by the aerial parts of the plants. Consequently the association of the various individuals together to form the plant community is largely the outcome of the fact that root competition is reduced to a minimum, this being often brought about by the roots of different species occupying different soil horizons.

The positions and structure of underground organs should also be considered from the point of view of their protective influence under certain conditions. A case in point is that of the heath fire which kills the surface-rooted *Calluna* while the *Vaccinium Myrtillus* and *Pteridium* with their deeply buried rhizomes escape permanent injury. Similarly, the positions of perennating buds, which carry on the growth of the plants from year to year, should be noted in relation to the possibility of their being damaged or destroyed by winter cold, drought, and the attacks of herbaceous animals, etc.

STUDY OF PLANT SUCCESSION

One should be continually on the look out for the evidences of plant succession which are to be found in practically any vegetation-covered area. Destructive forces are perpetually at work and these bring about the initiation of seres of various degrees of importance. It will usually happen that some, at least, of the plant communities that are receiving special attention will be definitely seral in character. On the other hand, they may appear to be seral communities and at the same time are, by the operation of some factor or factors, maintained in a relatively stable sub-climax state. Information on this latter point is often furnished by the fact that the influences which result in the sub-climax state, by preventing the succession from proceeding to its normal climax, are not uniformly in operation throughout the area. For instance, we have the case where grazed vegetation is separated by a fence from ungrazed vegetation. Detailed information relating to the successional features of cases of this kind can be obtained by fencing off an experimental plot as described above (p. 75). In regions where powerful physiographic or biotic influences are at work, numerous similar seres in various stages of successional development commonly occur. By the examination of a number of adjacent examples of such seres it is often possible to work out the whole sequence of changes which is passed through by the vegetation as it progresses from the initial colonization of the bare area up to the stable climax or sub-climax.

In cases where successional change is relatively slow or where one is doubtful if such change is taking place, what is known as the *quadrat* method may be resorted to. In this method, a square is marked out in the plant community by driving four pegs into the ground. For intensive studies of this kind the sides of the square are usually made 1 metre long. Having marked out the quadrat by means of pegs, which should preferably be of oak, tarred, or impregnated with paraffin wax to preserve them from decay, the positions of all the plants in the square are plotted to a reduced scale on squared paper. This procedure is repeated at intervals of one year or some other convenient period. In this way, after a prolonged interval of time, one is in possession of information regarding the changes that are taking place in the floristic composition of the section of the community covered by the quadrat.

A variation of this method of study is what is termed the *transect*. In the case of the *belt transect* a strip of definite width and of length suitable to the subject of study is marked out and plotted as in the case of the quadrat. If a *line transect* is being employed, a cord or measuring tape is stretched between two points and all the plants that occur on the line thus marked out are plotted to scale. Transects, when carried out, along with the study of habitat factors on areas showing zonation of vegetation, form a convenient way of illustrating the broad relationships between plant communities and particular habitat factors. As in the case of the quadrat, transects when permanently marked out and periodically examined yield information relating to successional changes that may be taking place.

The study of plant succession must always be conducted in conjunction with the study of habitat factors, as the real problems involved are not so much concerned with the changes that take place in the vegetation, as with the causes which bring about these changes. When studying succession consideration must be given to the question as to what species are available for colonization or entry into the community, as this will always have important bearing on the ultimate course of any particular sere.

Correlation of Results

In the foregoing pages the chief lines along which practical work in the field should be directed, have been pointed out. The outcome of such work is that one is provided with certain information, some of which is detailed and some of which is general in character, regarding the ecological features of the vegetation of the area studied. The data so collected have to be considered together and correlated, with a view to explaining as far as possible the particular characters of the plant communities present, in terms of the habitat factors operating. The consideration of habitat factors and the results of the study of successional features should help to throw light on the past histories of these plant communities and to some extent on their future fates. Complete conclusions cannot be reasonably expected, and it may be necessary to study a number of similar areas before anything approaching definite information is obtained. The important thing is to collect trustworthy data and to form ideas; the latter will become clarified as further work is carried out and will eventually lead to a more complete understanding of the problems of the subject.

A preliminary consideration of one's results should always be carried out as soon as possible after each stage of the field work has been completed, as one frequently finds that further information regarding certain features is needed. In this way each step can be, as far as possible, completed in its turn and the waste of time and trouble caused by having later to go back and repeat earlier stages of the work will largely be obviated.

Photography.—A camera forms an important item in the equipment of the ecologist. It should be light, have a good lens and be capable of obtaining views of both distant objects and of objects within about two feet of the camera.

When studying the vegetation of an area, photographs showing the appearance and distribution of the various plant communities are extremely useful when considering field notes at some later date. Also, when taking such photographs it is always advisable to make full notes stating what is shown in them. The exact position of the camera when taking a photograph should be recorded in order that others may, if it is thought advisable, be taken in the future from exactly the same position. Such series of photographs may yield valuable information concerning successional changes that may be taking place.

Close views of interesting features are often useful as illustrations to field notes, and may later yield information which was overlooked at the time when they were taken.

CHAPTER IV

THE VEGETATION OF GREAT BRITAIN

THE ecologist working in Great Britain is fortunate in that he has at his disposal, within a comparatively small area, a vegetation which is composed of a varied series of different plant-community types. This is partly due to biotic influences, and partly the result of diversity of topographical and geological features.

The vegetation covering most of the country is made up of a complex assortment of plant communities, the characters of which are largely the outcome of man's modifying influences. Anything approaching a complete account of even the more important of these communities would require a volume far larger than this present one for its accommodation. As we have only a few pages remaining at our disposal we obviously cannot do more than briefly consider the more important types. These types possess sufficient individual characteristics to render them reasonably distinct from one another. At the same time when one comes to study them in the field it will be found that they are accompanied by countless other communities which are intermediate in grade and which often form apparent or definite seral connexions between one type and another.

WOODLAND VEGETATION

The woodland vegetation of Great Britain belongs to two plant associations, namely the deciduous forest and the coniferous forest associations respectively. It is certain that at one time a great deal more of the country was under forest than is the case at the present day. Man's activities have nearly always, until quite recently, resulted in the destruction of woodland, and the consequence is, that at the present day, very little of the original primeval forest remains. Considerable stretches of forest vegetation, however, are still in existence as, for example, the Wyre Forest, the New Forest, and others. These, of course, have from time to time suffered a large amount of human interference in the way of felling, replanting, etc. In spite of this, however, they resemble to a considerable degree the original vegetation in regard to their floristic compositions, and consequently they are referred to as being *semi-natural.*

The deciduous forest in Great Britain comprises consociations having various species as dominants, the distribution of which depends chiefly upon edaphic causes. Over the greater part of England and southern Scotland, oak forest appears to be the climax vegetation type. In this the dominant tree is one or other of the two indigenous oaks namely, *Quercus sessiliflora* and *Q. robur.* These two species are fairly easily distinguished one from the other by their foliage, *Q. sessiliflora* having leaves with simple bases to their laminae and bearing on their under surfaces multiple hairs. The leaves of *Q. robur*, on the other hand, have auricled bases to their laminae and hairs, when present, are simple in character.

Q. sessiliflora woods occur on the shallow siliceous soils in the more hilly districts of the country, whereas those dominated by *Q. robur* are typically found on the deep clay and sandy soils of the Midland and Southern lowland districts. This distribution is very noticeable, for example, as one passes from the Cheshire plain to the hill slopes of the Pennines. On the deep glacial-drift soils of the former, the woods are almost invariably dominated by *Q. robur*, while on the shallow soils of the latter we find *Q. sessiliflora* as the typical dominant. Between the two occur woods of a transition type showing a mixture of the two species and their hybrids. Woods dominated by *Q. robur*, for reasons which are in the main connected with their situation, show in general a greater profusion of undergrowth than those dominated by *Q. sessiliflora*, and the shrub stratum is usually much better developed in the former than in the latter. The commonest species of the shrub layer is the hazel (*Corylus avellana*), while bracken (*Pteridium aquilinum*) is frequently a prominent species in the ground flora of both types of oak wood. The ground flora of the upland *Q. sessiliflora* woods usually contains a number of species typically found in heath communities ; for instance, bilberry (*Vaccinium Myrtillus*) is often conspicuously present, the shade-tolerating proclivities of this plant rendering it eminently suitable for such a situation. *Q. sessiliflora* forest is to be found extending up hill-sides to an altitude of from 1,200 feet to 1,500 feet. Up to 800 feet the trees flourish and grow to a moderate size, above this level wind usually begins to show signs of having a deleterious effect on them and they gradually become more and more stunted with increased altitude, until they thin out in an open scrub as their upward limit is reached.

Above the limit of oak woods, birch woods appear to have been widely distributed as the climax vegetation at one time. Such upland climax birch forest is still to be found in Scotland and in a few places in the north of England. In these woods the rowan or mountain ash (*Sorbus aucuparia*) is frequently present. In upland regions from which birches are now absent, this latter species commonly occurs on crag faces or is to be seen sparsely scattered over the mountain slopes above the limit of oak forest. Birch woods also are of frequent occurrence in lowland situations, but these, for the most part, will be found to be seral communities marking a stage in the succession leading to a climax having some other species, as for instance, the oak or possibly pine as dominant.

The deciduous forest association is also represented in England by consociations dominated by ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*). These communities, especially the latter, are usually associated with calcareous soils, although in areas where it reaches its greatest development beech forest may be found on non-calcareous loams. Beech forest forms the characteristic vegetation of the escarpment slopes of a large part of the chalk downs in the south of England. It occurs from about the middle of Sussex and stretches in a westerly direction, reaching its greatest development in West Sussex and Hampshire. As we pass still farther west into Wiltshire, beech tends to disappear while ash becomes the typical dominant on limestone soils. Beech trees, when growing in close canopy, form almost pure woods and in relatively young woods cast a very deep shade so that very few herbaceous plants are able to exist and form a ground flora. In older woods the canopy opens out somewhat and undergrowth appears. In addition to shade, an important factor in limiting the ground flora of beech woods appears to be the dense occupation of the upper layers of the soil by beech roots. The yew (*Taxus baccata*) is commonly associated with the beech and occasionally forms a subordinate tree stratum ; this species may be present even in dense beech forest, but is always local in occurrence. Where the beech trees are more widely spaced, ash, white beam (*Pyrus Aria*) and hazel (*Corylus avellana*) are commonly found in association with it.

The dependence of beech forest for its existence on edaphic causes is strikingly suggested by the fact that, on some parts of the Hampshire Downs, as one passes from the escarpment slopes of the hills and over the tops on to the dip slopes, woods dominated by the oak (*Quercus robur*) make their appearance. This appears to be due to the fact that weathering is less active on the dip slopes than on the escarpment slopes, with the result that on the former leaching has produced altered soil conditions, an important one of which is a reduction in the calcium carbonate content of the upper soil layers, which appear to favour oak as the successful dominant. Human activities may also have played a part in bringing about this change in the dominant species.

A characteristic feature of parts of the Downs is the presence of almost pure yew woods. These yew woods are what may be termed migratory communities as they apparently develop and then degenerate and frequently die out. Their development takes place in the shelter of scrub vegetation of either juniper or hawthorn, the spiny nature of which protects the yew seedlings from destruction by rabbits, which are frequently a serious pest on the Downs. The yews grow up above the scrub vegetation and cause its disappearance as a result of the dense shade they cast. Degeneration of the yew wood finally results from old age, regeneration from seed being prevented chiefly by rabbits, the activities of which are no longer held in check by the presence of a protective prickly scrub (see Watt, 1926).

On the slopes of the limestone hills of the north and west of England, ash woods are commonly to be found. They are especially well developed in the Peak District of Derbyshire, extending up the hillsides to an altitude of about 1,000 feet, above which is a zone of hawthorn scrub. Associated with the ash are usually the wych elm (*Ulmus montana*) and the hawthorn (*Crataegus oxyacantha*), and these become dominant when the ash trees are removed, in a way similar to that in which a birch community often springs up on the site of an oak wood after the oaks have been felled. Unlike the beech and the oak, the ash regenerates itself readily from seed, thus in an ash wood it is common to find an abundance of ash seedlings and young trees

Besides showing this distribution in relation to calcareous soils, ash frequently occurs as dominant on soils of a non-calcareous nature where soil conditions are wet. In this respect its soil requirements appear to resemble those of the alder (*Alnus rotundi-*

folia) and associated with that species and with certain willows it forms the characteristic fringes of trees that mark the courses of streams.

Alder is a common dominant of tree communities in low-lying water-logged situations. Such alder woods are seral in character and mark a stage in the succession which normally progresses towards drier habitat conditions and climax oak forest.

The coniferous forest association, as far as remnants of primitive pine forest are concerned, is now very restricted in its distribution in Great Britain, being confined to a few areas in the central part of Scotland. The dominant tree of these Scottish pine woods is not the ordinary form ot *Pinus sylvestris* that is to be found in various parts of England, but is the variety *scotica* of that species and has shorter needles and assumes a more pyramidal form of growth.

Pinus sylvestris in the south of England has been extensively planted on the sandy siliceous soil areas. In such situations it appears to thrive as it does also on similar soils in various parts of the Midlands. In the south it is in many places producing numerous seedlings and rapidly spreading by this means over heath land. This so-called sub-spontaneous pine forest has every appearance of being a climax community on these porous siliceous soils and probably should be considered as such.

HEATH AND GRASSLAND

Heath vegetation is widely distributed on the sandy soils of central and southern England and on the lower hill slopes in the west and north. It is invariably associated with acid soil conditions. Further, on chalk, where leaching has resulted in a non-calcareous surface soil, a particular mixture of heath and calcicole vegetation known as 'chalk heath' occurs. In western coastal districts with a distinctly oceanic climate as, for example, in Cornwall, heath is probably a climatic climax type of plant community. Elsewhere in the country heath communities are for the most part probably occupying areas that were once oak forest but from which man's destructive activities have resulted in the removal of the trees. This deforestation of sandy soil regions and their subsequent invasion by heath species has resulted in a degeneration and podsolization (see p. 54) of the soil so that conditions have become unfavourable for the regeneration of oak trees. That this heath vegetation cannot be truly regarded as a climax is evident from the already-mentioned fact that pines, when available, can invade it and eventually become dominant upon it. Birch also is frequently able to gain entry into heath communities and to form a type of open woodland, the exact status of which is doubtful.

The commonest dominant on heath is the ling (*Calluna vulgaris*) with which in drier situations is frequently associated the heather (*Erica cinerea*); this last species often becomes the sole dominant over considerable areas. As we have already seen, bilberry (*Vaccinium Myrtillus*) is usually present in heath communities, becoming a seral dominant after destruction of the *Calluna* by fire (see p. 53). Bracken also, which is a common constituent of the ground flora of oak woods, is usually more or less in evidence on heath land. This plant, which grows and spreads with renewed vigour after heath fires, should probably be looked upon as a survival from the original woodland which previously occupied the sites of most of our heaths.

True heath only occurs on relatively dry soils on which but a few superficial inches of peat are formed. Its developmental history is different from that of moorland vegetation which, although frequently similar floristically to heath, is always developed under conditions which give rise to peat of considerable thickness.

Heath often shows modifications as a result of the intense operation of certain habitat factors. We have several times touched upon the effects of burning; grazing, as we have seen, may also bring about striking changes such as the replacement of *Calluna* as dominant by some other species. Continued grazing by sheep may lead to a sub-climax type of community with *Vaccinium Myrtillus* as dominant. Heavy grazing by rabbits eventually brings about the degeneration of *Calluna* and the consequent change from *Calluna* heath to grass heath dominated by such species as *Festuca ovina* and *Agrostis tenuis*. It will thus be realized that grass heath and ordinary pasture land are closely related, both of them largely owing their existence to continued grazing.

MOORLAND AND MOUNTAIN VEGETATION

The term moorland, as it is generally used, is somewhat indefinite in its meaning. It is often indiscriminately applied to vegetation dominated by *Calluna vulgaris* and *Vaccinium Myrtillus* irrespective of the character of the underlying soil. We have seen that such communities, when present on relatively dry siliceous soils on which only a few inches of peat accumulate, are really heath communities. Moor, or moss as it is sometimes locally called, is characterized by the presence of a thick pure peat soil, the depth of which in some places is as much as 30 feet. Floristically, moor shows a considerable degree of variability which is largely the result of local differences in soil-water content and in climatic factors.

Moorland can be divided into two definite types, namely the lowland type and the upland type. Although plant communities on these two types may be very similar in composition, they differ from each other in both origin and status. Lowland moors are seral communities occurring on peat accumulations which have developed during the filling up of lakes by reed swamp and later by fen vegetation. The peat accumulates and its surface gradually rises higher and higher above the level of the ground water so that a drier acid upper horizon is formed on top of the neutral fen peat. On this acid peat a heath type of vegetation becomes established and is frequently dominated by *Calluna* in its drier parts, and by such species as *Erica tetralix*, the cotton grass *Eriophorum angustifolium* and the moor grass *Molinia caerulea* in its wetter parts. A still later stage in the succession is usually marked by the appearance of birch trees and often pines, if seed of the latter is available, so that the moorland passes over to a forest climax. Lowland moors of this type are to be found in various parts of the country, as for example in the New Forest, and in the western parts of Lancashire.

Upland moor appears to be a climax type of vegetation which develops on level or gently sloping ground under the moist cold conditions of upland regions, of which examples are the Pennine plateau, the north-west of Scotland, and Dartmoor. On the flat tops of the Pennines, for instance, extensive areas of moorland dominated by the cotton grass (*Eriophorum vaginatum*) occur, and this plant has been responsible for the accumulation of peat layers varying in thickness from 5 to 30 feet. On many parts of the Pennines the upper courses of small streams have cut back into the peat and formed drainage channels through it. On account of this drainage the habitat has become drier and the cotton grass has been largely replaced by bilberry giving a vegetation type known as bilberry moor. Other characteristic species associated with these desiccated peat areas are the cloudberry (*Rubus Chamaemorus*) and the crowberry (*Empetrum nigrum*). At lower altitudes in the southern Pennines, *Calluna* becomes dominant on the drying-out peat, giving true heather moor as opposed to many upland stretches of heath which go by that name.

In the north-west of Scotland, in parts of the Lake District and in other regions where conditions are cold and wet, one frequently finds the chief dominant and peat-forming species to be *Scirpus caespitosus*. This scirpus moor may also pass over into heather moor, as is the case with cotton-grass moor, where drying out of the peat occurs. Associated with the *Scirpus caespitosus* are usually to be found the mat grass *Nardus stricta* and the rush *Juncus squarrosus*.

On gently sloping mountain-sides under acid and moderately moist soil conditions, *Nardus stricta* is frequently dominant on a characteristic type of mountain grass-land known as *Nardus*-moor. In place of this *Nardus*-moor, under drier soil conditions, *Calluna* heath or, where grazing is heavy, a dry type of pasture dominated by such grasses as *Deschampsia flexuosa* and *Festuca ovina* often occurs. In mountain and hill regions, in fact, owing to numerous local topographical variations in habitat factors, one often finds whole series of moorland, heath, grass-land and woodland communities existing side by side within a relatively small area.

In the higher more exposed parts of the mountains of Wales, the Lake District and Scotland, there is to be found a type of vegetation known as *Arctic Alpine* vegetation. It is so designated because it contains a mixture of species some of which are characteristic of the alpine regions of Central Europe and some of which are typically inhabitants of Arctic regions. Among the more distinctive species of this zone of vegetation are various Saxifrages, dwarf willows of which the commonest is *Salix herbacea*, and such species as *Alchemilla alpina*, *Carex rigida*, *Lycopodium Selago*, *Lycopodium alpinum*, the viviparous variety of *Festuca ovina*, and the moss *Rhacomitrium lanuginosum*.

Alchemilla alpina, the alpine lady's mantle, together with *Festuca ovina* var. *vivipara* and other subordinate species, forms a typical natural arctic-alpine turf on the shallow immature soils of mountain-tops between altitudes of 1,200 feet and 3,000 feet. On the higher exposed summits, owing to intense weathering, the soil frequently consists almost entirely of rock fragments, and is known as mountain-top detritus. This supports a characteristic vegetation which, owing to the extreme exposure, is composed of stunted, low-growing plants, whose aerial parts rarely project more than about an inch above the surface. Here the destruction of patches of the vegetation by frost, wind, and rain is frequently liable to take place, so that often only an open type of community is able to maintain an existence. Woody species such as *Salix herbacea*, *Vaccinium Myrtillus*, *Vaccinium Vitis-idaea*, and *Empetrum nigrum* have extensive underground rhizome and root systems by means of which they are anchored to the substratum, only sending up at intervals stunted shoots. Associated with these are the mosses *Rhacomitrium lanuginosum*, *Polytrichum alpinum* and certain herbaceous plants such as *Festuca ovina*, *Carex rigida* and *Lycopodium Selago*. In the more remote parts of the Scottish highlands there also occur in these detritus communities, *Silene acaulis*, *Azalea procumbens*, *Saxifraga oppositifolia* and other less common species.

FRESHWATER HYDROSERE COMMUNITIES

In many parts of the country there are to be found stretches of reed swamp and other related vegetation, covering considerable areas where soil conditions are permanently wet. These, in spite of their apparent stability, must be regarded as seral stages in the succession which has its commencement in the aquatic plant communities of shallow water and ends with climax forest or with some sub-climax type of vegetation. In this succession we have reed-swamp, fen, and tree communities dominated by alder and various willows.

Reed-swamp communities are of common occurrence in the form of fringes along the margins of ponds, lakes, and slow-running streams. They are, however, developed more extensively and cover large areas along the margins of the shallow lakes known as broads which are to be found in the eastern parts of Norfolk and Suffolk.

The depth of the water in which reed swamp occurs is an important factor in the determination of the dominant species, and as a result of this the vegetation usually shows well-marked zonation in relation to this feature. *Scirpus lacustris* and *Equisetum limosum* in most situations occur as dominants in the deeper water, and so form the outermost vegetation fringe. Associated with them is often the white water lily (*Castalia alba*). In the shallower water the reed grass (*Phragmites vulgaris*) is in many places dominant, although considerable variations occur in different regions, and communities dominated by *Typha latifolia*, *T. angustifolia*, *Sparganium ramosum*, *Menyanthes trifoliata* and certain sedges, are of widespread distribution.

The water, in which the reed-swamp communities described above develop, contains adequate dissolved bases, but owing to anaerobic soil conditions the dead remains of the plants continually accumulate as mild peat. The surface of the submerged soil is thus gradually raised until a state is reached in which the water-level varies from a few inches above it in winter, to a few inches below it in summer. When this stage is reached a type of vegetation known as *fen* develops, and is composed chiefly of communities dominated by *Cladium Mariscus*, by such grasses as *Molinia caerulea*, *Phragmites vulgaris*, *Phalaris arundinacea*, *Glyceria aquatica*, by the rush *Juncus subnodulosus* and by the bog myrtle, *Myrica gale*. In course of time fen gives place to either woodland or moor. Where the succession leads on to woodland, the alder (*Alnus rotundifolia*) becomes dominant and with it usually occurs the ash (*Fraxinus excelsior*), the guelder rose (*Viburnum opulus*), the two buckthorns (*Rhamnus Frangula* and *R. catharticus*) and an occasional pedunculate oak (*Quercus robur*). This type of woodland if left to develop naturally will, as soil continues to accumulate and become drier, lead on to climax forest dominated by *Quercus robur*. On the other hand, as has already been pointed out on page 89, fen, when occurring in western districts with high rainfall, often leads on to the formation of moor, owing to the accumulation of acid peat on top of the original mild fen peat.

MARITIME VEGETATION

The vegetation along our sea coasts includes salt marsh and the plant communities of sand-dunes and shingle beach. In the case of salt marsh the various communities present are stages in hydrosere development, but they differ from those of reed swamp and fen chiefly on account of the fact that the water, in which the succession is initiated, is salt. Salt marsh is the characteristic vegetation of the mud flats that develop along the shores of the estuaries of our slow-flowing rivers. It forms considerable areas of turf dominated by *Festuca rubra* and *Armeria maritima* which are valuable as sheep pastures. The typical course of salt-marsh succession has already been outlined on page 56.

The successions on sand-dunes and shingle are xerarch in character, beginning as they do on a substratum which, owing to its extreme porosity, is often very dry.

On sand-dunes, colonizing plants in addition to having to cope with shortage of soil water have to be capable of withstanding the effects of the instability of the soil which results from its liability to be moved by wind. The marram grass (*Ammophila arenaria*) is by far the most usual dominant species. This plant, owing to its xerophilous nature and to its extensive rhizome and root systems, is able successfully to withstand drought and also to bind together and stabilize the sand on which it grows. Another grass of similar capabilities which usually occurs on sand-dunes and may become locally dominant, is the sea couch grass (*Agropyron junceum*). As the sand becomes stabilized and gradually richer in organic matter, other species gain entry and the vegetation commonly passes over into heath or scrub.

At some places along our coasts, as for example near the estuary of the Dovey in Wales, the shore is continually being extended in a seaward direction by the accumulation of shingle. Above the high-water mark this shingle becomes colonized by such species as *Arenaria peploides*, *Silene maritima*, *Suaeda fructicosa* and others. In the early stages of the succession an open type of community persists for a long time, the plants being rooted in the crevices between the pebbles. In time these crevices become filled with accumulated sand and plant remains and gradually the vegetation extends to form a complete covering to the shingle. Later stages in the succession are often very similar to those following the colonization and stabilization of sand-dunes.

HISTORICAL DEVELOPMENT OF THE VEGETATION OF GREAT BRITAIN

The vegetation of Great Britain has undergone marked changes during recent geological times since the last glacial period when the greater part of the country was under an ice sheet. Information regarding these changes has been obtained from the study of plant remains preserved in various peat deposits. The lowest horizons of many of these deposits contain the remains of arctic species and were obviously formed shortly after the final retreat of the ice. Above these lie a series of successive horizons composed of the remains of the various types of vegetation, which in turn appeared and disappeared one after another throughout the period during which the peat was accumulating. Of recent years the British peat deposits and those of various parts of Europe have been made to yield far more facts about the post-glacial history of vegetation than was previously the case. This has been largely due to the development, in Sweden (see Erdtman, 1928), of the pollen statistical method of investigation, which was devised by the late Professor Lagerheim, of the Botanical Institute of the University of Stockholm. In this method the frequencies of the preserved pollen grains in the different peat horizons are taken as indices of the abundance of the species to which they belonged; and its success is due to the fact that these pollen grains are often recognizable when other plant structures are almost completely disintegrated.

Besides revealing the lines along which the history of vegetation has passed since the last Ice Age, the study of peat deposits has told us something about the climatic changes that have taken place since that time. The result of this is that a series of climatic periods is now recognized.

For some thousands of years during the final retreat of the ice sheet, there extended what is termed the *preboreal* period. During this time the climate gradually changed from arctic to sub-arctic, and the vegetation, at first tundra, gradually passed over into birch forest with abundant willows, and pines appeared. Next came the *Boreal* period in which the climate was Continental in character, being warm and dry, and the land was dominated by forests of pine and birch. During this period the hazel, elm, oak, and alder appeared. The vegetation of the first half of the boreal period seems to have been characterized by the extensive occurrence of dense, more or less pure hazel forest. This hazel forest, after persisting for some time, apparently rapidly degenerated, probably owing to climatic changes, and in many parts of the country it was replaced by pine forest. This in turn appears to have degenerated also and, as the climate changed to the warm moist oceanic type of the *Atlantic* period which followed, the alder became predominant and oak forest largely replaced the pine and birch. In central Scotland, however, the pine remained and has in fact persisted until the present day. During Atlantic times, which probably extended from about 5,000 to 3,000 B.C., most of the trees at present occurring in the British vegetation were present, including the lime, which apparently reached a maximum about the middle of the period. There then followed a second warm dry period, the *sub-boreal* period, of about 1,000 years' duration, towards the end of which there are indications that the beech may have first made its appearance in the country (Erdtman, 1929). From this time until the present day the climate has been moist and cooler, giving us the *sub-Atlantic* period during which the oak, alder, and birch have apparently been the most abundant trees, the oak being the most extensive climax dominant.

The foregoing extremely abridged account can obviously only be taken as an indication of some of the historical features that have marked the development of our forest vegetation. It must, however, be admitted that some of these even are of a highly hypothetical character. The story as yet is not complete and probably never will be, though a great deal of work on the examination of peat deposits still remains to be done. This, when finished, will, without doubt, fill in many of the gaps that exist in our knowledge of what is unquestionably an extremely interesting branch of ecology.

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